Assessment of farming systems and cover configuration options that enhance natural regulation of herbivorous arthropod abundance in maize-fields

by

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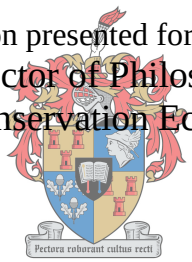

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Declaration

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Dissertation format

This dissertation is presented as a compilation of 6 chapters. Each chapter is introduced separately and is written, including reference citing and list of bibliography, according to the style of the journal Agriculture, Ecosystems and Environment.

The following chapters have already been submitted for publication in journals

Chapter 3: Otieno NE, Pryke, JS, Jacobs, SM. The top-down suppression of arthropod herbivory in inter-cropped maize and organic farms: evidence from $\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses. *Journal of Agronomy for Sustainable Development.*

Chapter 4: Otieno NE, Jacobs, SM, Pryke, JS. Influence of farm structural complexity features and farming systems on insectivorous birds' contribution to arthropod herbivore regulation in maize fields. Biotropica.

General summary

Maize, *Zea mais*, is grown globally and is a leading staple crop in sub-Saharan Africa, where it crucially sustains many household economic and nutritional needs, and the continent's food security. However, its production is curtailed by damage from a range of herbivorous arthropods, undermining its potential to fulfil increasing demand from a growing population. In Kenya, maize is produced primarily by small-scale subsistence farmers who have limited economic capacity for commercially-based arthropod herbivore control. Whereas the scale of future crop arthropod damage is projected to increase due to global warming, low economies of operational scale undermine many farmers' ability to increase their response investment to forestall anticipated crop losses. This calls for measures for crop-field arthropod control that are affordable yet affective for sustainable maize production. I investigated a range of agronomic management practices that may be applied in fostering natural suppression of arthropod herbivore abundance across 16 non-Bt maize-fields in western Kenya. I assessed how structural configurations and cover elements including hedgerows, on-farm trees, crop-cover patterns, woodlots and maize cover proportion enhance farm-level habitat complexity to attract predatory arthropods and insectivorous birds for top-down suppression of herbivorous arthropods. I compared effects of these variables on abundance, richness and diversities of arthropod and birds species between organic and conventional farming systems and between monocultured maize versus maize inter-cropped with legume crops. To assess potential for herbivorous arthropod reduction rates, I analysed $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures to track maize carbon through herbivorous arthropods to arthropod predators, and also established a bird exclusion experiment to test insectivorous birds' contribution to reducing arthropod abundance. By grouping farms into structural clusters, I further tested how arthropod and bird assemblage turnovers differed between local farm-level and wider spatial scales and along a heterogeneity gradient. Organic rather than conventional farming was more supportive of local-scale arthropod abundance, together with inter-copping, but not at wider spatial levels. However, organic farming was less important than crop diversity in boosting insectivorous bird abundance and richness. Herbivorous arthropods were significantly attracted to fields with higher maize cover proportions especially on conventional farms, suggesting susceptibility of monocultured maize to proliferous arthropod herbivory. Higher hedgerow volume, tree densities and larger woodlots enhanced all arthropod guild and bird aggregations at both spatial scales. Although the bird exclusion experiment proved insectivorous birds' linkage to herbivorous arthropod suppression at local-farm level, this effect was not evident at wider spatial scales. Stable

isotope analyses revealed a stronger predator-herbivore trophic linkage under inter-cropping systems, with lepidopteran herbivores the most significant consumers of both maize and legumes. On the other hand, ants showed the best capacity to suppress maize-consuming arthropods while wasps and beetles would best reduce legume consumers. The findings demonstrate that there is a wide range of farm-level habitat management practices for enhancing habitat complexity to boost natural top-down herbivore suppression across maize-fields, but greater effectiveness is achievable through synergistic application of measures rather than individualistic approaches. Furthermore, a multi-spatial scale strategy in applying appropriate techniques would maximize landscape resilience against herbivorous arthropods.

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Opsomming

Mielies, *Zea mais*, word wêreldwyd gekweek en is 'n belangrike stapelvoedsel gewas in sub-Sahara Afrika, waar dit baie huishoudelike ekonomiese en voedingswaarde behoeftes onderhou, en die vasteland se voedselsekerheid. Produksie word egter belemmer deur skade van 'n verskeidenheid van herbivoriese arthropoda, wat die gewas se potensiaal om die toenemende aanvraag van 'n groeiende bevolking ondermyn. In Kenia word mielies hoofsaaklik geproduseer deur klein-skaalse bestaansboere wat beperkte ekonomiese kapasiteit het vir kommersieel-gebaseerde beheer van herbivoriese arthropoda. Terwyl toekomstige arthropod skade aan gewasse voorspel word om te vererger as gevolg van aardverwarming, sal lae ekonomieë van operasionele skaal baie boere se vermoë om hul beleggings verminder in arthropoda-beheer om verwagte verliese verhoog te kortwiek. Dit vra vir alternatiewe oplossings vir gewas-veld arthropoda bestuur wat effektief en bekostigbaar is vir volhoubare mielieproduksie. Ek het 'n reeks van agronomiese bestuur praktyke ondersoek wat toegepas kan word vir die bevordering van natuurlike onderdrukking van herbivoriese arthropoda in 16 nie-Bt mielie-velde in Wes-Kenia. Ek het beoordeel hoe strukturele konfigurasies en dekking elemente insluitend kantheinings, plaasbome, gewas-bedekking patrone, brandhoutpersele en mielies bedek-verhouding plaasvlak habitat kompleksiteit verbeter deur predatoriese artropoda insekvretende voëls te lok vir top-af onderdrukking van herbivoriese artropoda. Ek het die effekte van hierdie veranderlikes ondersoek op oorvloed, rykdom en diversiteit van arthropod en voëls spesies tussen organiese en konvensionele boerdery stelsels en tussen enkelgewas mielies teenoor mielies gegroei tussen gewasse. Om potensiaal vir herbivoriese arthropoda verminderingstempos te assesseer, het ek $\delta^{13}C$ en $\delta^{15}N$ stabiele isotoop waardes ontleed om mielie koolstof deur herbivoriese arthropoda tot arthropoda predatore te volg, en het ook 'n voël-uitsluitings eksperiment daar gestel om te toets insekvretende voëls se bydrae tot die vermindering van arthropoda oorvloed te bepaal. Deur plase in strukturele groepe te plaas, ek verder getoets hoe arthropoda en voël aggregasies verskil tussen plaasvlak en breër ruimtelike skale langs ’n gradient van heterogeniteit. Organiese eerder as konvensionele boerdery was meer ondersteunend van plaaslike-skaal arthropod oorvloed, tesame met wisselbou, maar nie by breër ruimtelike vlakke nie. Organiese boerdery was egter minder belangrik as gewas diversiteit in die bevordering van insectivorous voël oorvloed en rykdom. Herbivoriese arthropoda was aansienlik aangetrokke tot velde met hoër mielie bedekkings proporsies, veral op konvensionele plase, wat dui op vatbaarheid van enkelgewas mielies teen hoë arthropoda herbivorie. Hoër kantheinings volume, boomdigthede en groter brandhoutpersele versterkte alle arthropod gilde en voël aggregasies by beide ruimtelike

skale. Hoewel die voël-uitsluiting eksperiment bewys dat insekvretende voëls gekoppel kan word aan herbivoriese arthropod onderdrukking op plaaslike vlak, was hierdie effek was nie duidelik by breër ruimtelike skale nie. Stabiele isotoop analise het 'n sterker predator-herbivoor trofiese koppeling geopenbaar onder inter-gewas stelsels, met sprinkaanagtige herbivore die mees beduidende verbruikers van beide mielies en peulgewasse. Aan die ander kant het miere die beste kapasiteit gewys om te onderdruk mielie-vretende arthropoda te onderdruk terwyl wespes en kewers sal beste peulgewas verbruikers verminder. Die bevindings toon dat daar 'n wye verskeidenheid van plaasvlak habitat bestuur praktyke vir die verbetering van habitat kompleksiteit om natuurlike top-af herbivoor onderdrukking op mielie-velde ’n hupstoot te gee, maar groter doeltreffendheid is haalbaar deur sinergistiese toepassing van maatreëls eerder as individualistiese benaderings. Verder, 'n multi ruimtelike skaal strategie om toepaslike tegnieke toe te pas, sal landskap elestisiteit teen herbivorous grondgeleedpotige diere maksimaliseer.

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Chapter 1: General introduction and literature review

1.1 Crop pests and global climate change

Global demand for food production is expected to increase by 75% between 2010 and 2050 as a result of increasing human populations (FAO, 2009a; Popp et al., 2013; Cerda et al., 2017) with the demand for cereal crops alone projected to increase by 42% (FAO, 2009b) . However, crop loss due to arthropod pests remain a hindrance to meeting such demands and presents a major threat to food security. For instance between 2005 and 2010 alone, the world incurred an estimated annual loss of 20 – 35% of major staple crops to pest damage (Cerda et al., 2017). Changes in climate due to increasing global warming is one of the key drivers of crop damage from arthropod herbivory (Cannon, 2004; Thomas et al., 2012; Wheeler and Braun, 2013; FAO, 2014). One of the reasons is that rising temperatures are responsible for increased reproduction rates and geographical range expansion for many arthropods (Rosenweig et al., 2001; Cannon, 2004). For instance, Ong'amo et al. (2016) indicated that the number of generations of some species of maize pest in the Noctuidae family (Lepidoptera) is expected to at least double within the next 3 decades. Increased temperatures are also associated with arthropod feeding rates and in a study by Deustch et al. (2018) to project future crop loss scenarios, arthropod pests are expected to consume 10-25% more maize, wheat and rice for every 1ºC rise in global climate temperature. Additionally, temporal shifts in herbivore and predator phonologies due to changing weather conditions could undermine predators' natural capacity for top-down regulation of herbivore populations, further aggravating the risk of pest proliferations (Andrew and Hughes, 2005; Pauls et al., 2013). Such frequent climate and weather variability will also distort the timing of agronomic operations, thereby worsening shortfalls in overall crop yields and earnings from rain-dependent crops such as maize (Olayide et al., 2016; Omoyo et al., 2015).

The impacts of global climate change are expected to be particularly acute in low income tropical regions, and for a number of reasons. Firstly, tropical regions are more vulnerable to climate shocks and weather extremes due to their proximity to the equator (IPCC, 2007; Thomas et al., 2012; Teixeria et al., 2013). Secondly, although increasing the intensity of pesticide use is a possible solution, the projected increase in arthropod species and varieties will require a wider array of more expensive pesticides besides the negative ramificastions to human and wildlife health from the consequent environmental pollution (Bebber et al., 2014). Similarly, new bio-technological developments in transgenic crop varieties such as Bt-maize to resist pest attacks (Ebenebe et al., 2000; USEPA, 2000; Van den Berg and Ebenebe, 2001; Tefera et al., 2016) are still beyond the economic reach of most small-scale farmers. Such genetically-engineered crops

have also proved ineffective against some arthropods after prolonged exposure across multiple, heralding evolution of resistance in some target pest species (Andow, 2008; Obonyo et al., 2008; Tabashnik et al., 2013; Van den Berg, 2016). Transgenic crops are additionally viewed as bearing potential risks for long-term environmental and genetic contamination of native species of flora and fauna (Castaldini et al., 2005; Wu, 2006; Kunert, 2011; Siegwart et al., 2015). Furthermore, because small-scale maize farmers operate at small subsistence levels, they operate at comparatively weaker economies of scale and thus have limited access to financial credit, leading to low capacity for sustainable commercially-based arthropod herbivore management (FAO, 2009a; Huis and Meerman, 2010; Edame et al., 2011; Tefera et al., 2016). Relatively low literacy levels make it difficult still for most subsistence farmers to cope with technical challenges that characterize the dynamism, technology-driven and highly competitive nature of modern intensive farming (Davis et al., 2010). Therefore even though most African farmers have historically used a variety of indigenous knowledge and technologies to cope with seasonal dynamics of soil, water and crop-arthropod interactions (Boillat and Berkes, 2013), new forecasts on climate change impacts present a unique and particularly difficult challenge in the short and medium term. This has necessitated frequent adjustments to agronomic field operations such as onset of planting, weeding, in order to avert or minimize losses from crop failure and arthropod damage (Chidawanyika et al., 2012).

Therefore there is urgent need for more innovative but affordable and sustainable field management techniques to address the challenges that arthropods pose to maize production. In this regard and against the backdrop of a changing climate, adopting of habitat management practices that foster natural top-down control of arthropod herbivores by predators and parasitoids may be the most efficient and cost-effective strategy for minimizing crop loss, and particularly suited to low-income farmers in developing countries (Landis et al., 2000; Chidawanyika et al., 2012). This is because despite their relatively low technical and economic capacity, small-holder farmers remain the key food producers in such countries, being responsible, for instance, for an estimated 75% of overall crop production in sub-Saharan Africa (IFPRI, 2004; Chauvin et al., 2012; IFAD, 2013). Such farmers are not only critical to future food security on the continent (Sasson, 2012; FAO, 2014) but also constitute a prime target for capacity development for innovative, effective and sustainable techniques in integrated pest management (Edame et al., 2011; Sasson 2012).

1.2 Conservation field management methods and herbivorous arthropod regulation

There is growing evidence that structural configurations and cover patterns of agricultural landscapes have significant influence on corresponding assemblage composition and functional as well as spatial distribution of arthropod communities (Tilman et al., 1997; Thomson et al., 2012;

Chidawanyika et al., 2012; Wolts et al., 2012). For instance, more structurally complex farm habitats incorporating diverse or mixed crops, live hedgerows, on-farm trees and semi-natural patches either at the crop-field or farm-wide spatial levels, can support larger abundances and richness of vertebrate and invertebrate predator species. Such species utilize the farmland in a variety of ways such as foraging, breeding, burrowing or as refuges from predators (Benton et al., 2003; Fuller et al., 2004; Geiger et al., 2009; Rusch et al., 2010; Wolts et al., 2012). Similarly, farm habitats comprising fields of diverse crops in various sizes and patterns increase cover heterogeneity and offer opportunities for a more diverse range of species (Dassou and Tixier, 2016). Such an enhanced range of consumers increase trophic interactions as well as the chances of ecological services by some of the species, including pollination, pest regulation and nutrient cycling (De Groot et al., 2002). Botha et al. (2017) showed that maize-fields with greater patches of natural vegetation in their neighbourhood, particularly grasses, supported higher abundances of arthropod communities and enhanced arthropod-plant diversity linkages that are potentially beneficial for natural herbivore regulation. Similarly, Balzan et al. (2016) showed that maintaining semi-natural field-margin vegetation improved habitat complexity and was associated with higher arthropod parasitoid diversity. On the other hand, rate of crop damage by herbivorous arthropods increased at the landscape level with higher cover proportion of arable land when field margin vegetation was missing.

Organic farming is recognised as one of the field management practices that enhance habitat heterogeneity (Norton et al., 2009; Winqvist et al., 2011; Inclan et al., 2015). The system entails use of field methods of crop diversification such as inter-cropping or rotation, and occasional fallowing or maintenance of semi-natural vegetation strips and hedges besides minimal or non-use of chemicals for soil improvement, herbivorous arthropod or weed control (Beecher et al., 2002; Letourneau and Goldstein, 2009; Wolts, 2012). Thus organic farming landscapes are characterised by higher structural complexity that facilitates a boost in overall biodiversity in general and natural enemy populations in particular, thereby increasing trophic interaction that promote natural top-down herbivore population regulation (Letourneau and Bothwell 2008; Geiger et al., 2010; Winqvist et al., 2011). At the same time, non-use of chemicals in arthropod and weed control preserves a safe and healthy environment with limited negative impacts on early growth stages of the beneficial predatory arthropods (Desneux et al., 2007; Bommarco et al., 2012). Reduced application of inorganic nutrients, especially nitogen fertilizers, is considered a climate change mitigation measure because nitrogenous fertilizers conttribute to emmission of nitrous oxide which is a major grenhoiuse gas (Snyder et al., 2009; Stuart et al., 2013)e since it This is in contrast to the more conventional approach involving more intensive agronomic practices such as regular use of inorganic nutrient fertilizers, pesticides and herbicides, often in large-scale

monocultured fields with little or no marginal vegetation and no occasional fallowing (Beecher et al., 2002; Gibson et al., 2007; Norton et al., 2009).

Organic farming may promote arthropod herbivore suppression in various specific ways. For instance, inter-cropping maize with legume crops has been shown to enhance diversity of predacious arthropods and parasitoids (Landis et al., 2000; Benton et al., 2003; Letourneau and Goldstein, 2009) which are essential in the biological reduction of lepidopteran maize arthropod consumers (Khan et al., 2006). Specifically, when legumes such as *Desmodium uncinatum* are inter-cropped with maize, they have been shown to attract predacious insects that prey directly on the maize stem borer *Busseola fusca* Fuller (Lepidoptera, Noctuidae) (Ogol et al., 1999; Duale 2005; Cook et al., 2007). Such leguminous cover crops have also been demonstrated to facilitate increased soil fertility when the symbiotic rhizobic bacteria in their rot nodules fix free nitrogen into the soil (Biswas and Gresshoff, 2014; Ianneta et al., 2016). In their review, Peoples et al. (2009) estimated that for every tonne of dry matter shoot by crop leguminous crops, rhizobic bacteria can facilitate fixation of up to 40 Kg of nitrogen into the soil.

Further, Tixier et al. (2012) observed that habitat heterogeneity arising from mixing crops of diverse photosynthetic pathways has the additional benefit of reducing intra-guild predation incidents amongst predacious insects owing to presence of a wider herbivorous arthropod prey range, and this enhances potential of the predators' role as herbivore suppressers. In addition, cultural field practices such as crop rotation may provide temporal dimensions to crop-field diversification which has been shown to break herbivore reproduction cycles, further contributing to reduction in herbivore abundance (Weisz et al., 1994). Some scientists have however argued that organic farming is subordinate to conventional farming because of the former's lower overall crop yields in comparison to conventional farming methods which can boost yields through the use of inorganic fertilizers for soil improvement and chemicals to remove pests and weeds (Connor, 2008; de Ponti et al., 2012). Nonetheless, such contestations rarely take full account of the capital costs of production and environmental health *vis-à-vis* net returns for each of the two farming systems (Sudheer, 2013).

Besides organic farming, another field-scale habitat management method - "push-and-pull" - has shown demonstrable success in east Africa as an option for managing maize arthropod pests since the turn of the century (Cook et al., 2001). The method involves undertaking two complimentary agronomic practices simultaneously: on the one hand, "pushing" is achieved when maize is inter-cropped with other companion legume crops such as *Desmodium sp.*, which produce volatile chemicals to repel the maize stalk borer *B. fusca* from the plot. Concurrently, *Desmodoium spp*, being a cover intercrop creates a conducive habitat within the maize plot, for predacious arthropods and parasitoids such as ants, spiders and wasps. These predators further feed on borer

larvae, or, in the case of wasps, parasitize them, thus reducing infestation in the maize crop (Khan et al., 2006). On the other hand, "pulling" is achieved when a specific range of grass species such as Napier grass *Pennisetum purpureum* and Sudan grass *Sorghum sudanense* are planted along the plot borders, and these grasses become the new refuge for *B. fusca* "pushed" or repelled from the maize plots, but the grasses also produce sticky gum that traps *B. fusca* larvae and therefore arrests *B. fusca* larval development towards maturity (Cook et al., 2007).

The push-pull technique is a useful and environmentally safe option for controlling maize stem-borers and is potentially a cost-effective supplement to farming of transgenic maize varieties. However, since the technique focusses primarily on the plot-level spatial scale and targets only one pest species, broad-scale alternative techniques targeting multiple herbivorous consumers are needed to complement it. Accordingly, Winqvist et al. (2011) and Chisholm et al. (2014) showed that the benefits of habitat complexity management for biocontrol of herbivorous arthropod consumers, such as through organic farming, are likely to be more fully realized if complexity exists at both local-farm as well as at the landscape spatial scales. In support to this, Chaplin-Kramer et al. (2011) observed that landscape-scale rather than local complexity is particularly important in boosting higher abundances of specialist arthropod predators that are instrumental in herbivore regulation to minimize chances of pest outbreak. Further still, according to Tilman et al. (1997), habitat management practices that change functional rather than just compositional diversity at multiple scales are more likely to have tangible impacts on ecosystem processes driving overall natural suppression of herbivore abundance, as opposed to exclusively local-scale action that is more effective against specialist but not generalist herbivores (Dassou and Tixier, 2016). Therefore more studies are required to identify key structural and cover features that, in a spatially integrated manner, influence and enhance interactivity between arthropods predators and herbivores to reduce crop damage (Müller et al., 2010).

Like predacious arthropods, insectivorous birds' contributory role to herbivorous arthropod suppression may be enhanced by field management methods that increase overall habitat heterogeneity. These include maintenance of on-farm trees, hedgerows and uncultivated margins as these features provide extensions of the natural habitat for foraging and breeding or roosting (Hooks et al., 2003; van Bael et al., 2008) while also facilitating dispersal linkages across the farming landscapes (Munoz-Saez et al., 2017). However, insectivorous birds are still generally under-appreciated as agents of herbivorous arthropod regulation and are seldom incorporated in integrated pest management programs. As a result, very little effort is devoted to conserving birds in farmlands (Wenny et al., 2011) and instead, many farmers are more likely to allocate resources to pest-bird control (Taber and Martin., 1998; Boyce et al., 1999; Tracey et al., 2007). The main reason is the smaller number of studies to highlight insectivorous birds' significance in

herbivorous arthropod regulation, when compared to similar studies on predacious arthropods, particularly in the eastern tropics (Bianchi et al., 2006; Tscharntke et al., 2007; Rusch et al., 2016). Majority of the studies in this theme have been undertaken predominantly in the American regions (Tremblay et al., 2001; Perfecto et al., 2004; Borkhataria, et al., 2006; Johnson et al., 2009) while in Africa, scientific interest on birds' role in suppressing farmland herbivorous arthropod consumers is only beginning to take off and progress looks encouraging. For instance, Ndang'ang'a and Vickery (2013) quantified the contribution of insectivorous birds in controlling pests on the vegetable kale *Brassica oleracea acephala*, while Guenat (2014) examined the impacts of insectivorous birds, alongside other arthropod parasitoids, in controlling vegetable-damaging aphids under different agroforestry systems, and Milligan et al. (2016) assessed the role of birds and ants in controlling coffee pests on highland coffee in Kenya. No studies have, however, been conducted to assess the role of birds in reducing herbivorous arthropod populations on small scale maize farms in Africa. There is a need for more such evidence-based information because it has potential for use in farmer advisory on appropriate farming techniques aimed at attracting beneficial birds as part of integrated pest management.

The habitat management methods for boosting structural and cover heterogeneity to foster natural herbivore regulation, as outlined above, constitute a significant part of measures collectively referred to as conservation agriculture. This concept is gaining growing momentum, even for large commercial farms, as a means of mitigating and adapting to impacts of intensive farming, and as a solution to increasing impacts of climate change, rising costs of chemical inputs and the rapidly degrading agricultural environment (Giacomo et al., 2012; Shahid and Ahmed, 2014; Sain et al., 2017). Conservation agriculture as a structurally and culturally-encompassing farming concept is now widely recognized as a form of sustainable agriculture essential for future food security (Lobell et al., 2008; Pretty et al., 201l; FAO, 2013). Within the context of its use in this dissertation, the term "conservation agriculture" is underpinned by its definition as offered by the Food and Agriculture Organization of the United Nations (FAO, 2013).

1.3 Overall aim of the study

My main goal in this project was to assess key farm-level habitat structural configuration management systems that enhance habitat heterogeneity to drive composition, assemblage and trophic interactions of arthropods and insectivorous birds across non-Bt maize-fields so as to foster natural top-down arthropod herbivore regulation. I assessed these variables across a selection of maize farmed under organic versus conventional systems as well as monocultured maize versus those inter-cropped with legume crops in western Kenya. In assessing the overall impact of a range of arthropod predators at the same time as insectivorous birds on herbivorous arthropods, I

managed to present a broader perspective of key field management measures suitable for integrating biocontrol of arthropod herbivore abundance across non-Bt maze fields, as opposed to a focus on either one herbivore or predator species as has been the case in many past studies. The study is presented in six chapters and I outline below the specific aims of each, in realizing the overall study goal.

1.3.1 Specific objectives and structure of the study

Chapter 2: Influence of farming systems, cropping methods and habitat structure on assemblage composition of arthropods. In this chapter, I assessed how key farm-level structural features across maize-fields such as cover types and vegetation configurations influence abundance, species richness and diversities of predacious and herbivorous arthropods. I also evaluated how farming systems and cropping methods affect the role of such structural features on the arthropod assemblages and compositions. I undertook this evaluation to test the premise that in general, organic farming systems and mixed-cropping of maize with legume crops, for instance, may enhance habitat complexity (Norton et al., 2009) and therefore support higher abundances of predacious arthropods and increase their interactions with arthropod herbivores, thereby boosting natural regulation of herbivorous arthropod populations across maize-fields (Van den Berg et al., 2001; Gaigher et al., 2016).

Chapter 3: **Analyses of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes to assess role of predacious arthropods on arthropod herbivore suppression across maize-fields.** My objective in this chapter was to examine how predacious arthropods contribute to regulating abundance of maize-field herbivorous arthropods through the trophic chain linking predacious arthropods to herbivores and down to maize as a basal food source (Hyodo, 2015). To achieve this, I used $\delta^{13}C$ and $\delta^{15}N$ stable isotopes to track organic carbon from three main plant food sources: maize, legume crops and field margin plants (food sources), through herbivorous arthropods (primary consumers) up to the predacious arthropods (secondary consumers). For this purpose, I used a multi-source Bayesian mixing model to evaluate the relative contributions of maize (RCM) carbon to the predator diets (Ostrom et al., 1997; Phillips et al., 2005) and this allowed me to determine and rank consumers in terms of relative roles as potential pests or pest regulators. By comparing RCM between organic and conventional farms and between mono-cropped maize-fields and maize inter-cropped with legume crops, I further managed to evaluate the roles of farming systems and cropping options in optimizing predator roles in management of herbivorous arthropods across maize-fields.

Chapter 4: **Influence of farm structural features on insectivorous birds' contribution to arthropod herbivore suppression in maize-fields.** Birds are the most conspicuous vertebrates across many tropical landscapes, and many arthropods that constitute insectivorous birds' diets are

consumers of crops (Kellerman et al., 2008). However, birds are still little recognized as arthropod population suppressors when compared to predatory arthropods (Karp et al., 2014). In this chapter I aimed to investigate the role of insectivorous birds as contributors to the natural control of herbivorous arthropod populations across the fields of mono-cropped maize and those in which maize is inter-cropped with legume crops. I first assessed influence of habitat structural features and farming systems on composition and assemblage of insectivorous birds and arthropod herbivores. I then tested for covariation in abundance, richness and diversity of insectivorous birds and their potential arthropod herbivore prey and if this was underlain by any habitat structural variables, so as to evaluate the trophic linkage strength. I further established a bird exclusion experiment to more finely underscore the importance of insectivorous birds in impacting herbivorous arthropod abundance, in order to test any underpinnings of their contribution role to suppressing herbivorous arthropods. I then summarized how these direct and indirect assessments of insectivorous birds' contribution to such suppression is affected by habitat variables and how these interlinkages vary across farming systems and cropping methods.

Chapter 5: **Role of landscape-level habitat management action in driving natural arthropod herbivore regulation.** Habitat complexity at the local farming scale arising through diversified structural configurations is known to support greater aggregations and functional interactions amongst varieties of vertebrate and invertebrate species, many interactions of which may also support natural biocontrol of herbivorous arthropod abundance (Bianchi et al., 2006; Dominik et al., 2017). However, whether this is valid also at the larger beyond-farm spatial scale, especially on the maize landscape, is not always clear and this is the aim of this chapter. By clustering the 16 individual farms into 5 progressive clusters of structural and cover pattern complexity, I set the landscape-scale context within which I used data of the previous three chapters to evaluate if the effects of structural configurations on assemblage turnovers of arthropod herbivores and their predators, both vertebrate (insectivorous birds) and invertebrate (predacious arthropods) differ between the local farm level and the wider landscape spatial scales in terms of reduction in overall crop herbivory.

Chapter 6. **General discussion and synthesis of overall findings**. Here I present a discussion that synthesizes the findings from all the chapters of the study, putting each into the perspective of the extent to which the aims of the project are achieved, and offering insights as to how my findings compare against those from relevant previous studies. I end the chapter with conclusions of my key findings in this project and venture recommendations for future research directions in this theme.

1.4 Importance of the study

This study is significant in five main ways. Firstly, it presents a robust outline of key field management practices that are applicable in supporting natural suppression of herbivores that represent the greatest threat to production of maize, the most important staple crop in sub-Saharan Africa (Smale and Jayne, 2003). In light of the continued underappreciation of insectivorous birds' role in crop arthropod herbivore regulation (Sekercioglu, 2006; Johnson et al., 2009; Milligan et al. (2016)), his study makes an important contribution to this effort and should be an incentive to the promotion of insectivorous bird conservation across maize farms. Thirdly, the study is novel in being the first to compare arthropod predator and herbivore assemblage responses to habitat management impacts both at individual farm levels and at multiple spatial scales in non-Bt maize-fields. Fourthly, the project contributes to the limited number of past studies in sub-Saharan Africa involving application of stable isotope analysis to evaluate predator-herbivore trophic interactions on agro-ecosystems, the majority of which have mainly focused on aquatic habitats (e.g. Opiyo et al., 2016; Sitnikova et al., 2016) or rangelands (e.g. Boutton et al., 1983; Cerling et al., 2003; Bergstom, 2013) rather than on arthropods of maize-fields. Therefore the findings of this project contribute significantly to knowledge required in promoting environmentally sound and sustainable agronomic management practices for optimizing natural regulation arthropod herbivory, particularly on small-scale non-Bt maize farms. It also provides a technical foundation upon which more efficient and robust techniques such as stable isotope analyses may be applied in research to improve understanding of trophic interactions in agroecosystems to inform policy towards more efficient and sustainable crop pest management.

1.5 General notes

1.5.1. Fields and farms

Throughout the dissertation, the term 'field' is used to delimit areas covered by crop types (maize mono-crop or maize inter-cropped with legume crops for instance). 'Farm' is the collections of all crop-fields and structural and cover features together.

1.5.2 Organic and conventional systems

Although more details are provided under materials and methods sections in each of the chapters, 'organic farm' as used in the dissertation, generally refers to low-impact maize farming systems involving non-use of synthetic fertilizers to improve soil fertility (application of animal or plant-waste-based manures instead) and non-use of chemicals to control herbivorous arthropods, diseases or weeds, and this is in contrast to conventional farming where farmers grow maize

through routine application of synthetic or inorganic nutrients/fertilizers, and also control weeds, arthropod herbivores and diseases using herbicides and pesticides.

1.5.3. Repetitions

As the dissertation chapters are written in form of distinct parts in journal paper form, some aspects of methodological procedure are repeated due to overlaps in study subjects, sites and periods.

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Chapter 2: Influence of farming system, cropping methods and habitat structure on assemblage composition of arthropods

2.1 Abstract

Many arthropods inhabiting croplands constitute crop herbivores that are responsible for considerable economic losses particularly to small-scale farmers. Due to high costs of agrochemicals, however, such farmers face the challenge of being unable to sustain commercially-based pest management, and therefore require more affordable but effective alternative arthropod herbivore control systems. I examined the comparative roles of organic versus conventional farming systems and mono-cropped non-Bt maize versus inter-cropped maize, and how these influence arthropod guild response to structural configurations across the fields. Overall arthropod abundance was higher on organic than on conventional farms while the converse was true for herbivorous arthropods. Additionally, overall arthropod abundance increased with percent maize cover which also positively corresponded to species richness. Predacious arthropod abundance was higher under organic systems and correlated positively to hedgerow volume, maize cover and indigenous hedgerows while their diversity was higher on mixed than on mono-cropped maize-fields. Predacious arthropod species richness, on the other hand, was higher on fields surrounded by exotic compared to indigenous hedgerows. For herbivorous arthropods, other than farming system, assemblages only responded to maize cover proportion, which positively correlated to their abundance and species richness. I conclude that integrated low-impact agronomic practices involving organic systems, crop diversification and maintenance of adequate hedgerow quantities, whether native or exotic, are important in supporting higher predatory arthropod populations for enhanced potential benefit of top-down regulation of arthropod herbivory across maize-fields.

Key words: Non-Bt maize; Farming system, Conservation agriculture, Arthropod diversity; Rural development

2.2 Introduction

Agricultural land management practices have a strong influence on assemblage patterns and spatial distribution of arthropod communities within them (Macfadyen et al., 2011; Fischer et al., 2004). This is because such practices determine structural configurations and edaphic qualities of the cropland environment, leading to food resource dynamics that shape arthropod community structures and trophic interactions (Albane's et al., 2009; Birkhofer et al., 2011; Macfadyen, et al., 2011). Structural aspects that constitute such field practices include types, sizes or shapes of

various landscape elements such as crop-fields, hedgerows or uncultivated patches and margins (Bouton et al., 2009; Veres et al., 2013). On the other hand, qualitative practice aspects include temporal cropping systems and chemical interventions against arthropods, weeds and diseases as well as soil fertility treatments. The combined effect of structural and qualitative agronomic management systems determine habitat suitability and resource availability that ultimately determines arthropod assemblage turnovers predator-prey interactions (Li et al., 2007; Rooibos et al., 2014).

In the absence of chemical interventions, cropping characteristics such as geometric patterns or density, profoundly influence arthropod aggregations and distributions across farmlands. For instance, field-scale mixed cropping or farm-wide crop diversity promote structural attributes consistent with higher heterogeneity which is beneficial in attracting higher populations and diverse species of herbivore natural enemies (Weibull et al., 2003; Bianchi et al., 2006; Pryke et al., 2013). Semi-natural margins, hedgerows and grassy strips are also important as refuges, breeding or hibernation habitat for spiders and parasitoids in the medium term, since such features are temporally more persistent than most crops (Rusch et al., 2010; Gaigher et al., 2016; Botha et al., 2017). Conversely, widely-spaced crops planted on large monoculture landscapes may be more attractive to herbivorous arthropods and may increase the risk of proliferation of such consumers due to limited food variety options that face such species in such simplified habitats (Rusch et al., 2016).

Therefore, from the economic perspective, it is more beneficial, particularly to farmers constrained by unsustainable access to pesticides and herbicides, to adopt agronomic strategies that limit arthropod herbivore populations of herbivorous arthropods or weeds on croplands (Tscharntke et al., 2012). Such strategies form part of the practice of organic farming which involves non-use of chemical agents in controlling arthropod herbivores and weeds control or improving soil fertility (Palm et al., 2001). Instead, it uses organic nutrient inputs such as farmyard manure and crop residues in soil fertilization, along with inter-cropping, crop rotation and occasional land fallowing to enhance soil structure (Gomiero et al., 2011; Sani et al., 2017). The practice, which is growing increasingly attractive in developing countries, is considered as an option to small-scale farmers to compliment traditionally used methods of field management for minimizing pesticide costs by naturally controlling herbivorous arthropods through promoting habitat suitability for predacious arthropods (Norton et al., 2009; Gomiero et al., 2011).

However, despite the wealth of indigenous knowledge on field practices for top-down suppression of crop herbivory in many parts of Africa, climate change is expected to present more complex challenges to small-scale farmers. As an example, increasingly unpredictable weather patterns, upsurges in arthropod populations as well as projected shifts in phonological cycles of

herbivores *vis-à-vis* those of their predators, all threaten future agricultural production and food security (Thomson et al., 2012; Wheeler and von Braun, 2013). Farmers in this region therefore direly need technical advisory support systems towards appropriate field structural and cultural management systems that will maximize positive agricultural production outcomes within the backdrop of projected future scenarios of climate-mediated crop pest challenges (Giacomo et al., 2012; Sani et al., 2017).

My aim in this chapter was to assess how farming and cropping systems within small-scale non-Bt maize-fields influence composition and assemblage responses of arthropods to a range of structural features, and how this drives the potential for crop protection through natural regulation of herbivores by their predators. This was on the basis that low-impact farming and cropping systems that increase habitat structural complexity can support higher arthropod community structures and trophic linkages (Letourneau and Goldstein, 200; Macfadyen et al., 209) that foster natural suppression of arthropod herbivore abundance (Bianchi et al., 2006; Rusch et al., 2010; Veres et al., 2013). This will help to determine where we should focus local patch management to maximize impacts of arthropod predators in naturally reducing crop herbivory.

2.3 Matrials and méthodes

2.3.1 Study area

I undertook the study in Kakamega County, Kenya, located between 00°11'09"N-00°26'08"N and between 34°44'30"E-34°51'26"E (Fig 2.1) across a small-scale agricultural landscape dominated by non-Bt maize-fields interspersed with human settlements, riverine habitat and isolated patches of semi-natural or uncultivated scrub and bush (Garcia et al., 2009). Maize may be grown here in monocultures alongside or inter-cultured with a range of other semi-annual crops such as legumes, pulses or vegetables (Garcia et al., 2009). The most popular legumes for inter-cropping maize in Kakamega County are beans (Phaseolus sp, Fabaceae) and peas (Vigna sp, Fabaceae). The rainfall ranges from approximately 1,200-2,000 mm annually with bimodal distribution, the longer rain season occurring between March and May and a shorter one from August/September to October/November, while mean annual temperature is 21.4°C (Kenya Meteorological Department, 2017). Nearly all farmers grow maize in both seasons (Personal observation).

Although organic farming is not universally practiced in Kenya, farmers using the system apply only organic fertilizers such as animal manure and crop residues which additionally improve soil structure (Eden et al., 2017); plant multiple crops which are frequently inter-cropped and at times rotated across plots; and occasionally leave the land fallow during some seasons besides maintaining indigenous live hedgerows and woodlots on the farm. They also tend to keep a few

heads of livestock or poultry. Many of these practices have been used by farmers from earlier generations but are increasingly also being recognized by them as useful in strategically adapting to adverse effects of erratic weather conditions and declining soil quality as a result of prolonged use of inorganic fertilization in previous decades (Ministry of Agriculture Livestock and Fisheries, 2016). By contrast, farmers using the more conventional agronomic approach tend to have slightly larger croplands, predominantly apply synthetic fertilizers to grow crops in largely un-rotated monocultures, maintain little or no live hedgerows, allow no fallows nor uncultivated patches and are less likely to keep livestock (Personal observation).

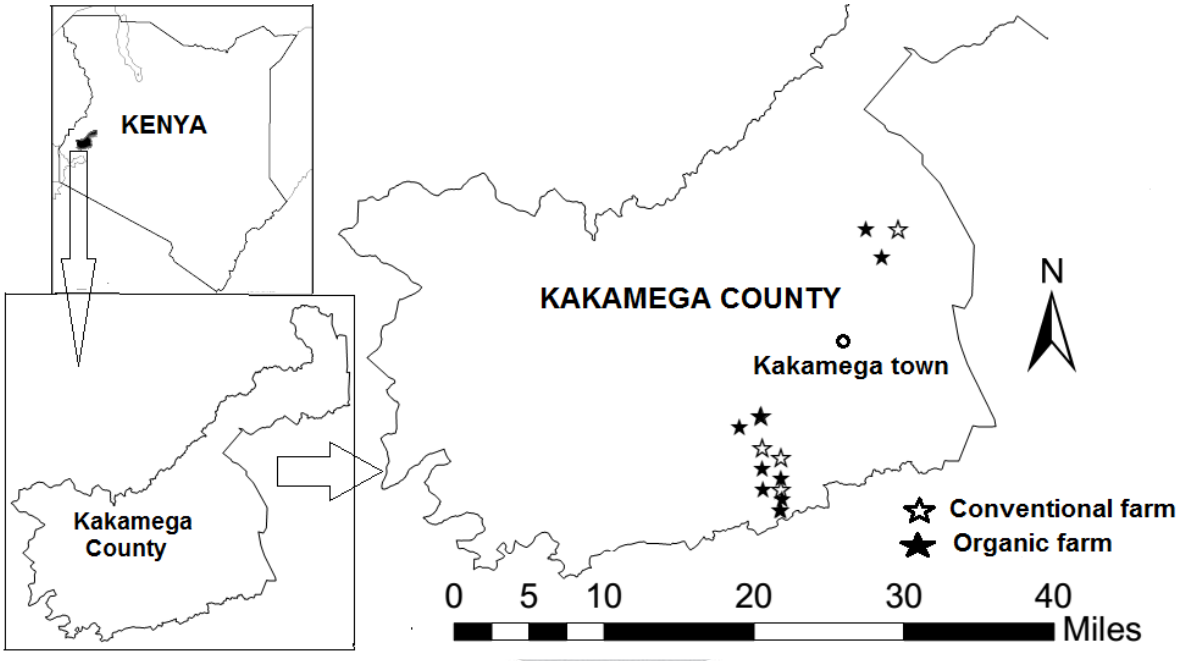

Fig 2.1. Study area showing locations of study farms by farming system categories.

2.3.2 Farm selection and topology

I selected farms on the basis of three basic topological criteria: presence of maize (non-Bt); maize farming system (those practicing organic agronomic methods versus those practicing conventional methods); and cropping methods (those on which maize is inter-cropped with legume crops versus those with monocultured maize). Thus I selected 16 farms randomly, of which 9 were organic and 7 conventional (Fig. 2.1), and 9 had inter-cropped maize while 7 were maize mono-crop fields so that eventually there were 3 mono-cropped organic, 6 inter-cropped organic, 4 mono-cropped conventional and 3 inter-cropped conventional fields selected (Table 2.1).

2.3.3 Sampling of habitat

I conducted field sampling during two maize planting seasons, from October 2015-January 2016 (short rain season) and March-July 2016 (long rain season). During each season, sampling was conducted at three crop stages: early crop (from germination to first weeding), mid-crop (from second weeding through flowering to cob formation) and at mature-crop (from cob hardening to harvesting). To assess actual farm features that drive arthropod assemblages or composition under influence of farming and cropping methods, I measured and determined a range of farm attributes which included maize cover as a percent of total farm acreage; hedgerow length; hedgerow height; hedgerow volume; and crop diversity. I determined hedgerow measurements using a 100-m tape measure and a metre rule. I measured hedgerows for total length, as well as height and width, each at intervals of 20 m along each side of the farm. I determined hedgerow length to the nearest metre and height or lateral width to the nearest centimetre. I also characterized the selected farms, which ranged from 0.6 to 9 hectares, for whether they were surrounded by indigenous or exotic live hedgerow, or if there was none. Independence of samples was ensured by maintaining a minimum of about 500 m inter-farm distance (Beecher et al., 2002). I also clustered farms into four blocks based on generally visualized contour of the landscape. The farm topologies (farming system, cropping method and hedgerow type) constituted the farm biotope variables while the farm habitat measures constituted the environmental variables (Table 2.1).

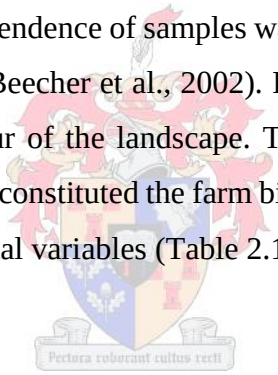

Table 2.1 Characterization features used for farm topology and habitat attributes. Regional groupings were based on observed general contour of surrounding farm landscape: A=undulating; B=gentle; C=steep; D=flat. No. crop-fields = total number of crop-type fields, including maize-field. Indicated in parentheses under hedgerow type are plant species dominating the hedgerows.

Farm number	Regional grouping	Maize cover (%)	Farming system	Cropping method	Hedgerow type	No. of crop-fields
F1	A	17	Conventional	Mono-cropped	Indigenous (*Tithonia sp.)*	2
F2	A	69	Organic	Mix-cropped	Exotic (Salicaceae, Mirb)	4
F3	A	63	Organic	Mono-cropped	Indigenous *(Tithonia sp.)*	3
F4	A	81	Conventional	Mix-cropped	Exotic (*Lantana camara*)	5
F5	A	66	Conventional	Mix-cropped	Indigenous (*Tithonia sp.)*	4
F7	B	39	Organic	Mix-cropped	Indigenous *(Draceana*	4
F8	B	28	Organic	Mono-cropped	None	2
F9	C	40	Organic	Mix-cropped	Exotic (*Lantana camara*)	2
F10	C	36	Organic	Mix-cropped	Indigenous (*Markhamia lutea*)	4
F11	C	22	Organic	Mix-cropped	Indigenous *(Draceana sp.*)	2
F12	B	15	Organic	Mono-cropped	Indigenous (*Tithonia sp.)*	5
F13	D	18	Organic	Mix-cropped	Exotic (*Lantana camara*)	6
F14	D	8	Conventional	Mono-cropped	Indigenous (*Markhamia lutea*)	3
F15	A	70	Conventional	Mix-cropped	Exotic (*Bougainvillea sp.*	3
F16	D	90	Conventional	Mono-cropped	None	1
F17	D	95	Conventional	Mono-cropped	None	1

2.3.4 Arthropods

I sampled arthropods using both standard sweep nets and un-baited pitfall traps. For sweep nets, 100 sweeps were made down the length of each field, to standardize the effort across all farms, sweeping on either side while walking at a steady pace (Gadagkar et al., 1990; Gardiner et al., 2005) Pitfall traps consisted of 70 mm diameter and 120 mm high plastic cups inserted in pits

with rims flush with ground surface (Pryke et al., 2016), and filled to one-third with 25% sodium chloride solution, with a conical plastic shield erected above each trap to guard against rain (Brown and Matthews, 2016). I randomly placed four replicate pitfalls along a diagonal line running across each maize-field, with the traps spaced at distance intervals that depended on maize-field size. I collected the traps after 3 days. When it rained to ground-run-off intensity, I discarded the affected samples and re-set the traps. During trap collection, I transferred the arthropod samples into zip-lock bags (Girard et al., 2011). To supplement sweep netting and pitfall trapping, arthropods were further sampled using actual search-and-pick on leaves, stems, flowers and cobs of cops using forceps, on the all maize plants along every 10th row of each field. In the laboratory, arthropods were sorted and identified to species or morphological species (Samways et al., 2010) except spiders, which were identified to Order. I also grouped arthropods into either of two broad feeding guilds: predominantly predacious (secondary and tertiary consumers) or predominantly herbivorous (primary consumers).

2.3.5 Data analyses

I analysed data in R software version 3.4.1 (R Core Team, 2017) within the lme4 and multcomp packages (Bretz et al., 2011; Bates et al., 2015). I analysed arthropod assemblages at two levels: overall and by guild. I determined hedgerow volume as a function of total length, mean height and mean lateral width (V = L(W*H)/n where V = volume; L = total length of live hedgerow around the farm; W = lateral width of hedgerow at each 20-metre interval; H = height of hedgerow at each 20-metre interval; n = total number of intervals. I estimated percent maize cover as proportion of maize crop on the whole crop-field as outlined by Thies et al. (2003) and scored crop diversity as total number of crop types, including maize with crops planted as a mixture within one crop-field were regarded as constituting one crop type. The habitat attributes constituted the environmental variables.

I pooled arthropod samples from sweep nets and pitfall traps and analyzed them together. Arthropod species diversity was assessed as the inverse of Simpson's dominance such that $D_2 = 1-\lambda$ where D_2 = species diversity and λ = Simpson's dominance index (Magurran, 1988; Pinkus-Rendón et al., 2006). I used Permutational Multivariate Analysis Of Variance procedure (PERMANOVA) in PRIMER version 6.1 (Primer-E, 2008), with unrestricted permutations in evaluating, in separates steps, main-effects of farm biotope factors: farming, cropping methods and hedgerow type (selected together as fixed-effect variables) on variation in overall, predacious and herbivorous arthropod assemblages (Primer-E, 2008). For significant effects of farm biotopes, I then performed one-way similarity percentage (SIMPER also on PRIMER+ 6.1) analyses with 999 permutations and Bray Curtis similarity measure, to distinguish arthropod families that

cumulatively contributed up to 90% of the abundance variations (Primer-E, 2008). Listing the arthropods into families was preferable to species *per se* because more than 50% of the species cumulatively contributed less than 1% each to the abundance dissimilarities between the farm biotopes.

I subsequently used Distance-based Linear Modelling (DistLM) in PRIMER with 999 permutations, incorporating all predictor variables (farm biotopes and environmental variables) to create a compositional similarity matrix of the study sites and show the environmental variables that best explained the matrix similarities or spatial variations. I normalized and square-root transformed environmental datasets prior to the DistLM procedures were run (McArdle and Anderson 2001). Environmental variable similarities were based on Euclidian distance and those of response (arthropod assemblage) variables based on Bray Curtis measures. DistLM was conducted stepwise with models selected using Akaike Information Criterion for small datasets (AICc) and I only selected predictor variables with significant effects at $p \leq 0.05$ from sequential tests (Trumpickas et al., 2011).

I assessed effects of farm biotopes and environmental variables on arthropod abundance species richness and diversity using Generalized Linear Mixed Models, GLMM fitted using Poisson error distribution with log-likelihood link function for abundance and species richness, and binomial distribution with logit link function for Simpson's diversity index (Bolker et al., 2009). I first tested variables for covariance using the Spearman correlation, as a result of which hedgerow length, *L* and height, *W* were eliminated, leaving volume, *V* as the sole hedgerow predictor variable. I included the final predictor variables (farming system, cropping method, hedgerow type, maize cover percent, hedgerow volume and total number of crop varieties) in the model as fixed effects, with farm number as a random effect to reduce farm-neigbourhood effects on arthropod assemblages (Raudenbush et al., 2000; Bolker et al., 2009). I used farm regional grouping term as an additional random factor in determining the response of Simpson diversity to the fixed variables.

2.4 Results

I identified a total of 212 arthropod species or morpho species from 15 orders comprised of 51 families across the farms studied (Appendix 1). Of these, there were 120 predacious species or morpho species representing 26 families, and 78 herbivorous species and morpho-species representing 32 families. Ants (Formicidae) were the most abundant and species-rich family across all farms and in all samples Table 2.2.

Table 2.2. Mean abundance per-sample and species richness within arthropod families identified. Arrangement is by decreasing rank of mean abundance.

Family	Mean abundance per sample	Species richness	Family	Mean abundance per sample	Species richness
Formicidae	240.0	56	Tenebrionidae	1.0	2
Grylloidae	47.5	3	Chrysopidae	0.8	2
Forficulidae	37.7	1	Nymphalidae	0.5	3
Arachnidae	26.7	1	Cicadellidae	0.3	10
Curculionidae	18.5	2	Meloidae	0.3	2
Acrididae	14.5	14	Merylidae	0.3	5
Carabidae	11.8	13	Nabidae	0.3	1
Spongiphoridae	10.0	2	Termitidae	0.3	1
Lycidae	5.5	1	Arctiitae	0.2	14
Chrysomelidae	5.2	16	Cercopidae	0.2	1
Pentatomidae	5.2	7	Coccinelloidae	0.2	1
Aphididae	4.8	5	Flatidae	0.2	1
Blattidae	4.7	5	Geometridae	0.2	1
Cicadidae	4.3	1	Hepiadidae	0.2	1
Labiduridae	3.8	2	Lagriidae	0.2	1
Noctuidae	3.7	15	Lasiocampidae	0.2	1
Coccinellidae	3.3	10	Miridae	0.2	1
Scelionidae	3.0	4	Mymaridae	0.2	1
Braconidae	1.7	6	Papilionidae	0.2	1
Eulophidae	1.7	2	Sapygidae	0.2	1
Ichneumonidae	1.7	3	Scoliidae	0.2	1
Thripidae	1.7	3	Staphynilidae	0.2	1
Melyridae	1.5	4	Tettigoniidae	0.2	1
Attelabidae	1.2	2	Timematidae	0.2	1
Cantharidae	1.2	1	Miridae	0.2	1
Chalcididae	1.2	4			
Hemerobiidae	1.2	2			

A summarised analysis of four of the most common maize pests in east Africa showed that conventional farmer and mono-cropped maize had higher abundances than organic and inter-cropped maize (Table 2.3).

Table 2.3. Some common arthropod pest species collected from the maize-fields with a comparative summary of abundances between farming and systems and cropping methods.

Maize pest	Abundance			
	Farming system		Cropping method	
	Conventional	Organic	Mono-cropped maize	Maize inter-cropped with legumes
Common field cricket (*Gryllus bimaculatus*, Laicharting - Orthoptera, Grylloidea,)	1	0	0	1
Maize Stem-borer (*Buseola fuscus* Latreille - Lepidoptera, Noctuidae,)	5	8	13	0
Spotted Stem-borer (*Chilo partellus* Latreille - Noctuidae,)	2	0	2	0
Lesser or Black Earwig (*Labia sp. – Dermaptera,* Labiduridae)	52	8	46	14
Maize Thrip (*Frankiniella williamsii* Stevens – Thysanoptera, Thripidae,)	3	5	7	1
Total	63	21	69	16

From PERMANOVA tests, farming system was the only farm type variable that showed a significant effect on determining assemblage variations for arthropods overall (F=1.389, p=0.032) (Fig. 2.2). Cropping method and hedgerow type had no effect (F=0.979, p=0.511; F=1.229, p=0.124). Subsequent SIMPER analyses indicated a total dissimilarity percentage of 73.1% between organic and conventional farming systems (Table 2.4).

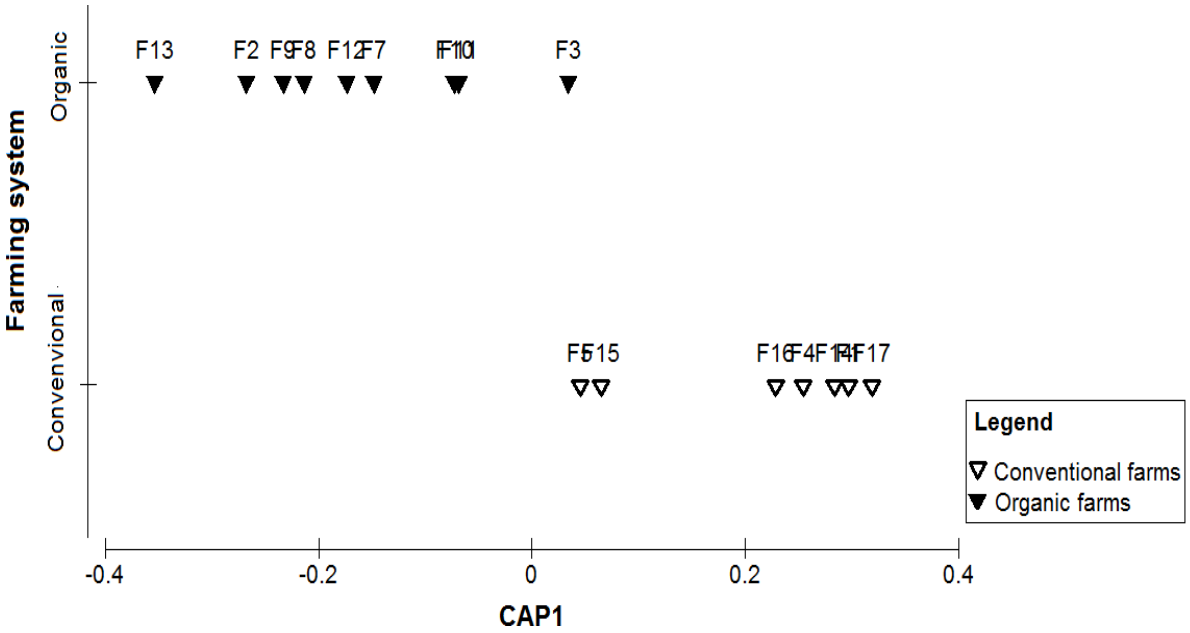

Fig. 2.2. Canonical analysis of principal coordinates (CAPs) of overall arthropod assemblage between the farming systems (organic versus conventional). Assemblage patterns were derived from Bray Curtis similarity resemblance matrix from square-rot transformed data.

Table 2.4 SIMPER analysis showing arthropod families that cumulatively contributed up to 90% to assemblage dissimilarities between the organic and conventional farming systems. *Diss/SD* = ratio of mean inter-group dissimilarity and associated standard deviation; *Contr* = individual percent contribution to assemblage dissimilarity; and *Cum* = cumulative percent contribution to assemblage dissimilarity.

Family	Diss/SD	Contr (%)	Cum %
Formicidae	30.2	45.6	45.58
Acrididae	6.2	4.9	50.54
Curculionidae	1.5	3.6	54.15
Gryllidae	1.7	3.4	57.53
Forficulidae	1.1	3.0	60.55
Chrysomelidae	3.3	2.3	62.89
Spongiphoridae	1.3	2.1	64.94
Carabidae	2.0	2.0	66.96
Araneae	1.5	1.9	68.93
Cicadellidae	1.8	1.7	70.58
Aphididae	1.9	1.6	72.15
Noctuidae	2.6	1.5	73.66
Coccinellidae	1.9	1.5	75.12
Pentatomidae	2.0	1.4	76.50
Merylidae	1.6	1.2	77.74
Chalcididae	1.9	1.2	78.97
Ichneumonidae	1.5	1.2	80.13
Blattidae	1.7	1.2	81.28
Braconidae	1.9	1.1	82.35
Tenebrionidae	1.0	0.8	83.16
Thripidae	0.9	0.8	83.94
Lycidae	0.3	0.7	84.68
Attelabidae	0.9	0.7	85.39
Scelionidae	1.2	0.7	86.08
Eulophidae	0.8	0.7	86.76
Cantharidae	0.7	0.6	87.32
Hemerobiidae	0.9	0.5	87.85
Nymphalidae	0.5	0.4	88.26
Termitidae	0.5	0.3	88.55
Melyridae	0.6	0.3	88.83
Timematidae	0.4	0.3	89.10
Arctiitae	0.4	0.2	89.33
Pentatomidae	0.4	0.2	89.56
Labiduridae	0.3	0.2	89.77
Nabidae	0.3	0.2	89.96
Mymaridae	0.4	0.2	90.12

From DistLM analyses of association of environmental variables to arthropod assemblage, hedgerow volume significantly accounted for 9.7% for the similarity matrices of arthropods overall and 10.4% of predacious arthropods. Percent maize cover accounted for 9.8% in explaining herbivorous arthropod similarity matrices (Table 2.5).

Table 2.5 Results of sequential tests from distance based linear models (DistLM) for significant effects of environmental variables on arthropod group compositional assemblage matrices across the farms. A significance level of $p<0.05$ was used.

Arthropod	Variable	AICc	Pseudo-F	*p*	Proportion (%) explained
Overall	Hedge volume	127.9	1.506	0.030	9.7
Predators	Hedge volume	127.5	1.623	0.033	10.4
Herbivores	Percent maize cover	128.3	1.529	0.022	13.9.

From GLMM tests, arthropod overall abundance was influenced by farming system and percent maize cover, while overall species richness was influenced by percent maize cover, crop diversity and hedgerow type with more species on exotic than indigenous-hedgerow farms (Fig. 2.3; Table 2.6). Post hoc Tukey Honest Significant Difference test (Tukey) showed that the greatest effect of hedgerow type on overall species richness was between indigenous and no-hedgerow categories ($t=2.561$; $p=0.026$). Overall diversity was enhanced by all farm biotope and habitat variables except crop diversity (Table 2.6).

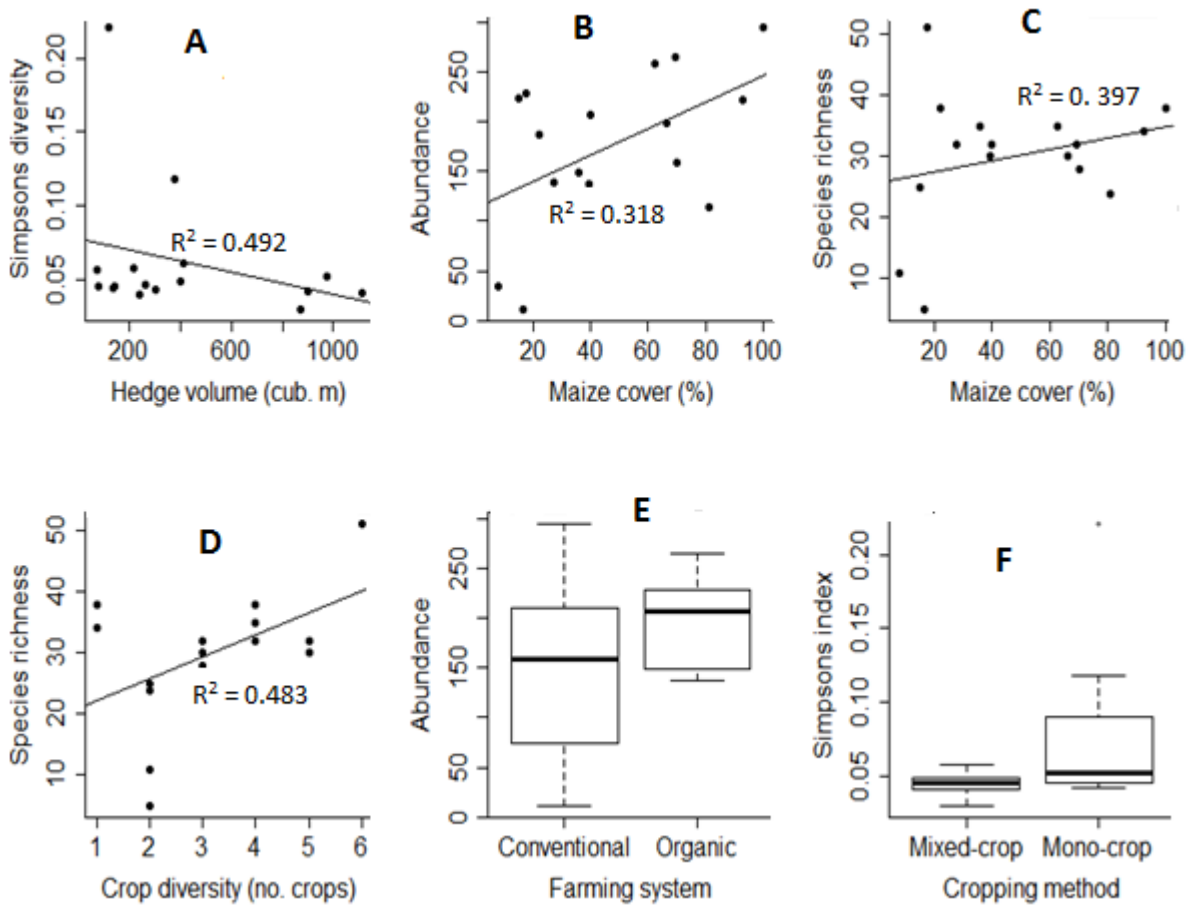

Fig. 2.3. Regression plots of effect of A) hedgerow volume on Simpson's diversity, B) maize cover on abundance C) maize cover on species richness and D) crop diversity on species richness; and box plots of role of E) farming system on abundance and F) cropping method on Simpson's diversity of arthropods overall.

In the case of predacious arthropods, abundance was influenced by maize cover, hedgerow volume, farming system and hedgerow type with significantly higher abundance associated with presence of indigenous hedgerows (Tukey t=-2.107; p=0.034). Their richness was affected by hedgerow type only (Table 2.6), the significant differences occurring between indigenous exotic and no-hedgerow (Tukey t=2.376; p=0.043) and between indigenous and no-hedgerow categories (Tukey t=2.722; p=0.017). Predacious arthropod Simpson's diversity was influenced by all predictive variables except crop diversity (Fig 2.4, Table 2.6).

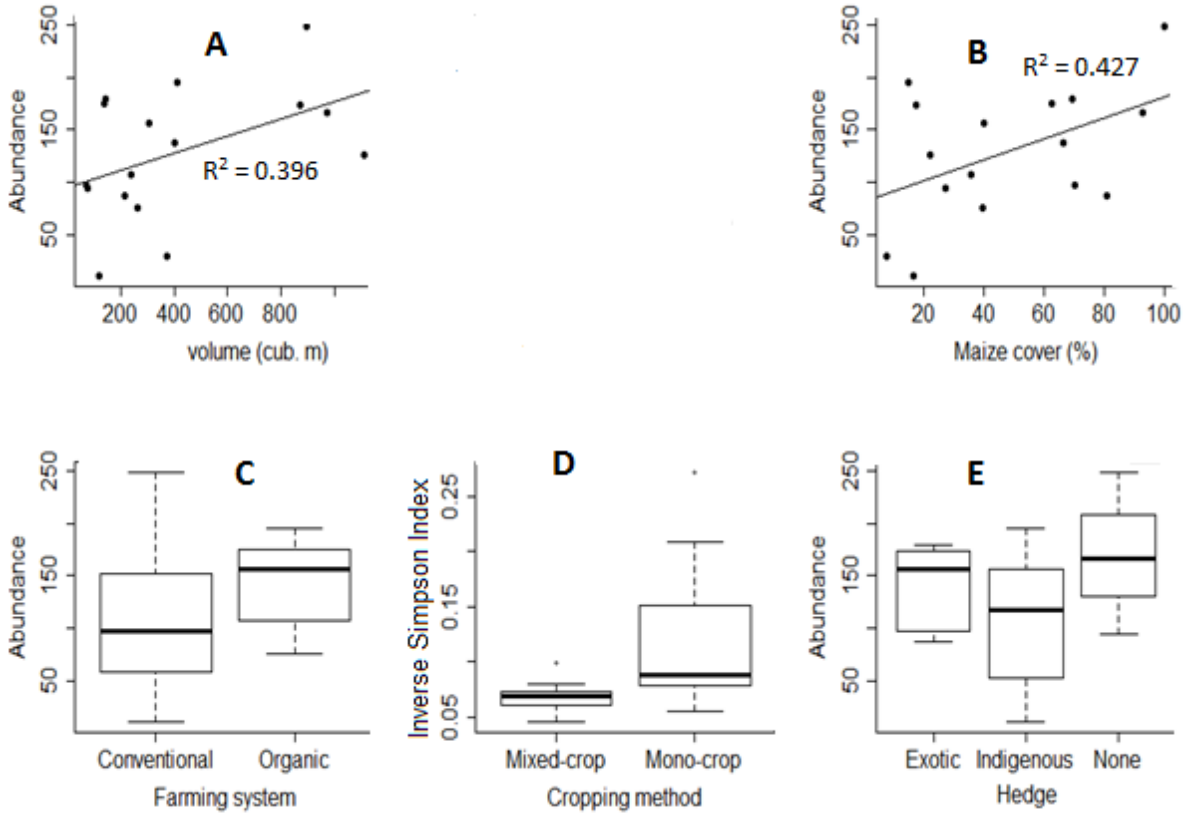

Fig 2.4. Regression plots of effects of A) hedge volume on abundance, B) maize cover on abundance, box plots of influence of C) farming system on abundance, D) cropping method on diversity and, E) hedgerow type on abundance of predacious arthropods.

Herbivorous arthropod assemblages were least influenced by predictor environmental measure variables, showing only positive responses of abundance and species richness to maize cover proportion, and a further positive response of abundance to conventional farming systems (Fig 2.5: Table. 2.6).

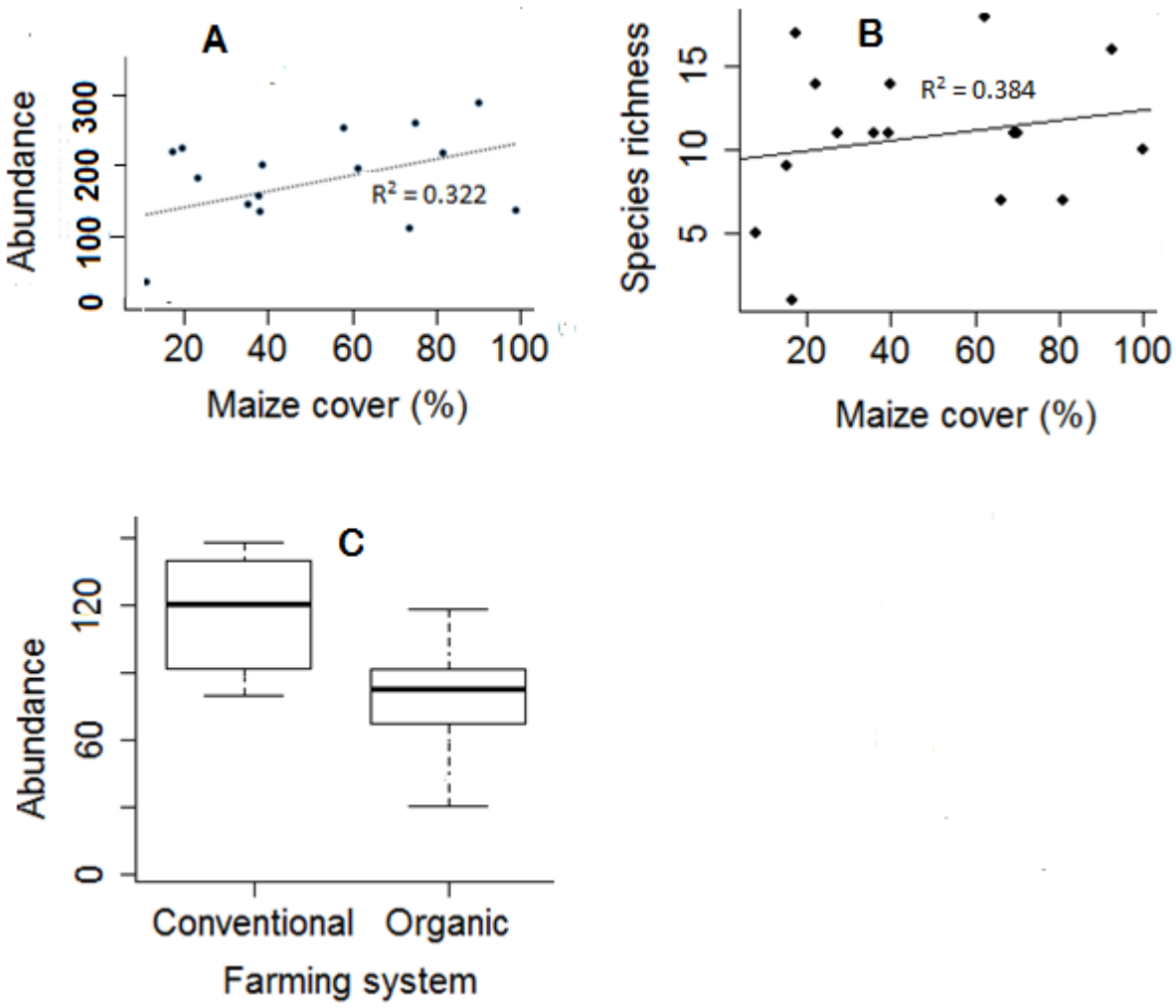

Fig 2.5. Regression plot of effects of A) hedgerow volume on abundance B) maize cover proportion on species richness and C) farming system on abundance of herbivorous arthropods.

Table 2.6 GLMM test of influences of farming-type and environmental measure variables on arthropod assemblages and composition. Crop diversity=total number of crop types on crop-fields on each farm. Significance codes: * p≤0.05; ** p<0.01; ***p<0.001.

Arthropod assemblage	Factor	Abundance	Species richness	Simpson's diversity
Overall	Farming system	<0.001***	0.056	0.007**
	Cropping method	0.927	0.498	0.036*
	Hedgerow type	0.075	0.037*	0.014*
	Hedgerow volume	0.109	0.447	0.024*
	Maize cover %	<0.001***	<0.017*	0.019*
	Crop diversity	0.714	0.050*	0.100
Predators	Farming system	<0.001***	0.232	0.003**
	Cropping method	0.330	0.105	0.003**
	Hedgerow type	0.042*	0.011*	0.005**
	Hedgerow volume	0.021*	0.272	0.114
	Maize cover %	<0.001***	0.241	0.072
	Crop diversity	0.978	0.252	0.515
Herbivores	Farming system	<0.001***	0.110	0.157
	Cropping method	0.284	0.313	0.551
	Hedgerow type	0.598	0.556	0.224
	Hedgerow volume	0.508	0.993	0.190
	Maize cover %	<0.001***	0.012*	0.680
	Crop diversity	0.247	0.301	0.039*

2.5 Discussion

Ants (Hymenoptera, Formicidae) were the most abundant group across all the farms studied, contributing nearly half of all arthropod compositional assemblage turnovers observed in this study. They were also represented by the largest number of species in all farms, making them, in addition to their high mobility, an excellent bio-indicator group for monitoring of landscape-level trends in agronomic management systems (as also suggested by Anderson et al., 2004; Underwood and Fisher, 2006). Their gregarious nature and ability to exploit prey at multiple horizontal and vertical spatial scales (Landis, 2000) additionally make ants superior in overall herbivore suppression. On the other hand, although they play a major predatory role across maize-fields, ants may have an indirect negative impact on crops by protecting some species of sap-sacking bugs such as corn-root aphids (*Aphis middletoni*, Thomas (Hemiptera, Apidae) and corn-leaf aphids (*Aphis sp*) from attacks by predators (Muray, 2007). Both of these bug species are maize consumers but are defended by ants within a symbiotic relationship in which the ants derive processed plant by-products from the bugs (Buckley, 1991; Young et al., 1997; Cranshaw and Redak., 2013).

After Formicidae, the four next most abundant arthropod families, namely grasshoppers (Orthoptera, Acrididae); weevils (Coleoptera, Curculionidae), crickets (Orthoptera, Gryllidae) and earwigs (Dermaptera, Forficulidae and Sphongiforidae) accounted for a cumulative total of 15% of dissimilarity between organic versus conventional maize-fields in the compositional assemblage matrix (Table 2). These are largely generalist herbivore or omnivore groups (Symondson et al., 2002; Dib et al., 2011), but each of the families has at least one species which consumes maize at some point in its life stages. Their combined numeric dominance which was second only to ants, underscores the trophic (and perhaps functional) dominance of these families as herbivores on the maize-fields when compared to the rest of the arthropods, 31 families of which shared a cumulative contributory total of just 28% amongst them. However, although grasshoppers occur in maize-fields throughout the maize growth period, only a few of the species encountered in this study constituted maize consumers. More notably, the potentially most destructive and invasive orthopteran, namely, locusts, were not observed (van Huis et al., 2006).

Although arthropod abundances and species diversities were positively influenced by farming and cropping systems that enhanced farm-wide structural heterogeneity, species richness was unaffected by farming or cropping regimes. This suggests that besides broadening niches for arthropod natural enemies (Bazzaz, 1975; Schmidt et al., 2005), organic farming and crop diversification also create an environment that reduces intra-guild dominance across the range of predators regardless of the available number of species. Furthermore, hedgerow volume showed a considerable positive influence on predacious arthropod assemblage, affecting both abundance and diversity and thus demonstrating, in addition to inter-cropping, the significance of farmland structural complexity in eliciting compositional response from this guild group. Therefore the collective positive influence of organic farming systems, inter-cropping maize and thicker hedgerows, on predacious arthropods underscores the fact that habitat complexity or heterogeneity is a keystone structural driver of natural enemy composition and assemblage at the spatial and functional scales. A similar observation was reported by Tews et al. (2004), Ratnadass et al. (2012) and Gaigher et al. (2016). Furthermore, Lichtenberg et al. (2017) also noted that organic farming enhances diversity of arthropods in general and predators in particular, making it a useful tool, along with crop diversification, in enhancing the ecological regulatory service of natural herbivorous arthropod reduction across farmlands.

Additionally, predacious arthropod's relatively higher abundance on farms surrounded by indigenous hedgerows points to the relatively higher longevity of these types of hedges when compared to exotic ones which are more frequently pruned by farmers for ornamental purposes (Personal observation), a practice that may constitute a form of anthropogenic disturbance to

arthropods. The conversely higher species richness of these predators on maize-fields surrounded by exotic rather than indigenous hedgerows, is more difficult to account for.

By contrast, for herbivorous arthropod assemblages, maize cover proportion was the only consequential predictor, irrespective of whether maize was inter-cropped or grown in monoculture; or whether the fields were surrounded or not surrounded by thick indigenous and exotic hedgerows. This was because of the significant trophic linkage of maize to most of the herbivores (Table 2) demonstrating the heavy dependence of arthropod herbivores on maize as a food source. This can be related to findings reported from a review by Meehan et al. (2011) from which the bird cherry-oat aphid (*Rhopalosiphum padi*, Linnaeus (Hemiptera, Aphididae) was observed to occur at higher abundances with increasing proportion of corn cover across a structurally simplified agricultural landscape in Midwestern USA. Dassou and Tixier (2016) also reported that local-scale habitat heterogeneity, which may be brought about by organic farming, tends to elicit a positive response more for specialist rather than for generalist herbivores. Similarly, Chaplin-Kramer et al. (2011) observed that herbivorous arthropod assemblages, particularly in terms of abundance abundance, are less likely to respond to habitat complexity than can predacious arthropods, with the implication that abundance of natural enemies in response to habitat heterogeneity does not always translate to herbivore suppression.

Herbivorous arthropods' higher abundance on conventional than on organic farms also underscores the attractiveness of such structural simple conventional systems to the crop consumers (Rusch et al., 2016), and risk of herbivore population build-ups. On the other hand, the concurrent increase in abundance of both predacious and herbivorous arthropods with increasing maize cover proportion points to the likelihood that aggregations of the predators on maize-fields is primarily in response to correspondingly high presence of their herbivorous prey. This further underscores the close trophic linkage between the two guilds and offers the opportunity for targeted management of habitat to maximize this connection for effective natural regulation of arthropod herbivores. Knowledge of finer details of such trophic linkage patterns including predator and prey phonologies for specific farming systems, may be further useful in timing the release of biological control agents, should such a less passive method become the preferred option.

Counterintuitively for hedgerows, there was lower abundance and richness of arthropods overall, on farms bearing indigenous rather than those with exotic or no-hedges. This was in opposition to effects of hedgerow volume and suggests three possibilities. First, although total available hedgerow surface supports higher predator abundances in particular (Wolts et al., 2012), indigenous hedgerows being typically thicker and less frequently pruned for maintenance, may be more impervious against free dispersal of some arthropod species into maize-fields (Sorribas et

al., 2016). This is in contrast to fields surrounded by the more routinely cropped exotic hedges, or by no hedges at all. Indigenous hedgerows might in this sense, help support a narrower range of species albeit at high concentrations. Alternatively, maize cover proportion, which also showed a significant influence on herbivorous arthropod assemblages, may override and diminish the significance of indigenous hedgerows especially since most farms surrounded by indigenous hedges were, in general, smaller and therefore had lower total maize cover. A third possibility is that when considered in overall, arthropod communities on maize-fields were comprised of more species of herbivorous than of predacious consumers.

2.5.1 Conclusion

These results demonstrate the significant roles of all four major farm-scape elements (low-impact/low-agrochemical use; inter-cropping; overall farm-wide crop diversification and maintenance of hedges of sufficient volumes) in boosting and maintaining sufficient combinations of arthropod compositions and assemblages for effective overall function of herbivore regulation. These practices are likely to achieve the best results if applied in conjunction rather than in isolation, as they are functionally complimentary in driving overall arthropod spatio-temporal community structures, dispersal and trophic interactions (Rusch et al., 2010). This is particularly so because no arthropod compositional element was uniformly influenced by all habitat variables, neither did any single management measure determine the entire suite of predator and herbivore compositional assemblages. For instance although proportion of maize cover elicited a positive assemblage response from both predacious arthropod and their herbivorous prey, indicating the close trophic predator-prey linkage, thick hedgerows were important intermediaries in sustaining spatial affinity to maize-fields. Therefore a synergistic habitat management strategy stands the best chance of ensuring sustainable top-down control of arthropod herbivores, and overall resilience of maize-fields to herbivorous infestation (Thies et al., 2003; Rusch et al., 2010). Letourneau et al. (2011) however cautioned in a meta-analysis review that despite there being a definite positive predator-prey interaction effect of plant diversification and structural heterogeneity under inter-cropping regimes or with the case of companion crops, in some instances, diversifying crops across fields so as to promote herbivore suppression can lead to lower yields as a result of reduced acreage for the main crops to give way to the companion crops or uncultivated marginal strips. A profitable balance might therefore at times have to be considered based on analysis of farming costs and the herbivore suppression benefits.

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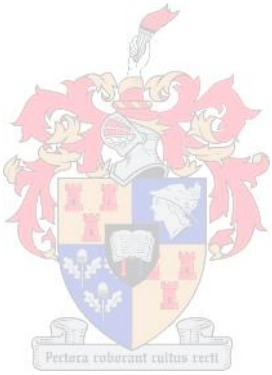

Chapter 3: Analyses of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes to assess role of predacious arthropods on suppression of herbivorous arthropods across maize-fields

3.1 Abstract

Maize is a staple crop in sub-Saharan Africa, mainly grown by small-scale farmers, but its production is undermined by many herbivorous arthropods, rapidly proliferating due to global warming. Coupled with escalating agrochemicals costs, such farmers need more affordable habitat-based alternatives for sustainable pest management. I used analyses of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes to assess roles of organic versus conventional farming systems (organic versus conventional) alongside inter-cropping versus mono-cropping methods, in fostering arthropod trophic linkages to non-Bt maize mono-crops, maize-legume inter-crops and field-margin plant food sources across small-scale farms in western Kenya. Arthropods were sampled using pitfall traps and sweep nets during two cropping periods, classified into predatory and herbivorous groups and isotopic analyses conducted to determine the predator-prey-plant food linkages using Bayesian mixing models. I found that Ants (Hymenoptera), earwigs (Dermaptera) and spiders (Araneae) showed the closest overall predatory trophic linkage to maize carbon while moth larvae (Lepidoptera) had the closest herbivorous linkage to maize. Trophic carbon from legumes inter-cropped with maize was most closely linked to wasps (Hymenoptera) and predacious beetles (Coleoptera) as predators, and to lepidopterans and phytophagous beetles as herbivores. Overall, the trophic linkage between predacious arthropod and their herbivorous arthropod prey was significantly better under inter-cropped than mono-cropped fields, but farming system alone had no significant impact. Therefore, generally, field management strategies for bio-controlling maize-consuming herbivores should, besides inter-cropping, target conservation of ants, earwigs and spiders due to relatively higher proportion of maize carbon signature or herbivore prey range in their diet. Similarly, wasps, ladybirds and ground beetles conservation will primarily help in reducing herbivorous consumers of legume crops. Finally, ants and spider conservation should be prioritized for field-wide regulations of overall populations of crop herbivores due to the broad range of their herbivorous prey items. Here I demonstrate how stable isotopes analyses can be used to characterize multiple-scale arthropod trophic interactions for underpinning hands-on conservation agriculture practices that foster enhanced ecological regulatory service of natural top-down herbivore suppression for sustainable farming of non-Bt maize.

Key words: Maize; Ecosystem service; Climate-smart; Isotope; Sustainable development

3.2 Introduction

Climate change due to increasing global warming is expected to accelerate population growth and spread of herbivorous arthropods and exert increased ecological stress on crops (Rosenweig et al., 2001; Cannon, 2004; Duale, 2005). The problem is expected to be particularly serious in tropical regions where agriculture is mainly undertaken by small-scale farmers with limited economic capacity for sustained chemical-based management of cropland herbivorous arthropods (IFPRI, 2004; Moyo, 2010; FAO, 2014). As a consequence, in Africa, overall agricutlural production will decline due to the urgent need for further investments in pest management, which is already unaffordable to most small-scale farmers (Sasson, 2012; FAO, 2014).

Strategies for biological control of herbivorous arthropod consumers through farm management practices to foster natural top-down control by predators and parasitoids offer one of the most sustainable solutions to the crop loss for low income farmers (Landis et al., 2000; Chidawanyika et al., 2012). This is supported by a large and growing body of field evidence which demonstrates that structural configuration of agricultural fields has significant influence on compositional and functional assemblages as well as distribution of arthropod communities. This is particularly so for predators and parasitoids that are beneficial in provisioning the ecological service of herbivore suppression (Tilman et al., 1997; Thomson et al., 2012; Chidawanyika et al., 2012; Wolts et al., 2012). Benton et al. (2003), Wolts et al. (2012) and Dominik et al. (2017) similarly observed that more structurally complex habitats or heterogeneous mosaics at the crop-field or farm-wide levels incorporating semi-natural patches, can provide more niches for a wider variety of herbivorous arthropod natural enemies that utilize them as foraging, breeding, burrowing, or refuge resources. Thus, one of the benefits of inter-cropping cereals with legume crops is that the inter-crops enhance habitat complexity that fosters functional diversity of arthropods (Landis et al., 2000; Benton et al., 2003; Letourneau et al., 2009; Wolts et al., 2012). For instance, some leguminous inter-crops are known to attract predacious insects that prey directly on arthropod that consume maize, such as stem borers *Busseola fusca* Fuller (Lepidoptera, Noctuidae) (Duale, 2005; Cook et al., 2007).

Further, as Tixier et al. (2012) pointed out, habitat heterogeneity arising from mixing crops of diverse photosynthetic pathways may provide the additional benefit of reducing intra-guild predation amongst herbivore natural enemies due to a wider range of prey options under such conditions, thus focusing the attention of the predators to their role as crop herbivore suppressers. Winqvist et al. (2011), Veres et al. (2013) and Chisholm et al. (2014) showed, however, that the benefits of habitat complexity for biocontrol of crop arthropod consumers are more likely to be realised if complexity exists at spatial scales wider than the local crop-field scale. Furthermore,

according to Tilman et al. (1997), habitat management practices that change functional rather than just compositional diversity are likely to have more tangible impacts on ecosystem processes such as herbivorous arthropod population turnovers, including their trophic interactions with predators.

One field-scale habitat management technique that has been successfully applied in the tropics to naturally suppress maize-consuming arthropods is the "push-and-pull" technique Khan et al. (2001). The method involves undertaking two complimentary agronomic practices simultaneously: on the one hand, "pushing" is achieved when maize is inter-cropped with other legumes companion crop such as *Desmodium uncinatum*, which produce volatile chemicals to repel *B. fusca* from the plot. At the same time, the presence of this companion inter-crop also contributes to plot-level habitat complexity which is attractive to arthropod natural enemies such as parasitic wasps, spiders, ants and predacious beetles. These facilitate predatory reduction of *B. fusca* populations in the maize crop (Ogol et al., 1999; Khan et al., 2001). On the other hand, "pulling" is achieved when a specific range of grass species such as Napier grass *Pennisetum purpureum* and Sudan grass *Sorghum sudanense* are planted along the plot borders, and these grasses release volatile chemicals that are attractive to the repelled *B. fusca* from the maize-field. The grasses simultaneously minimize their own vulnerability to *B. fusca* infestation by producing sticky gum that traps larvae to supress the latter's development to full life cycle (Khan et al., 2001). The puss-pull technique is a useful and environmentally safe alternative to application of agrochemicals for controlling maize stem-borers.

Because evaluating and quantifying trophic and biochemical linkages between arthropod herbivores and their predators typically entails highly intensive and often costly direct field observations, trials and monitoring before they are applied in arthropod herbivore management, they are often feasible for only one or a few herbivores at a time. Stable isotope analysis (SIA) method, however, offers a more robust, comprehensive and less sampling-intensive option for determining trophic linkages between a wider range of herbivorous consumers, their plant food source options and their predators across the plot, field or landscape spatial units (Post, 2002; Phillips et al., 2005). The technique allows underpinning of not only identity of consumer food sources but also evaluation of relative proportion of each food source in the consumer's diet for a specified duration (Phillips et al., 2005). This is because once incorporated into consumer tissue, isotopes maintain definite, predictable signature levels which change only in quantifiable incremental steps when the consumer's tissue is converted to that of its predator up the trophic chain. For instance, $\delta^{15}N$ isotope values generally increase by an approximate 3.4 parts per thousand (‰) and $\delta^{13}C$ by a near-unchanged value of 1.2 - 1.4 ‰ (Pillips et al., 2005; Fry, 2006). As such, a consumer's $\delta^{13}C$ signature is nearly the same as that of its basal (ultimate) food source. On the other hand, a consumer's $\delta^{15}N$ signature is always higher than that of its food sources due

to higher trophic fractionation of N making it possible to use $\delta^{15}N$ to infer a consumer's trophic position (Ferger et al., 2013; Hyodo, 2015). Further, $\delta^{13}C$ is instrumental in determining basal food sources and whether the basal food source is primarily photosynthetic along the C_3 pathway such as many woody plants and legumes; the C_4 pathways such as maize (Rubenstein and Hobson, 2004; Phillips et al., 2005) or the Crassulacean Acid Metabolism pathway, as in the case of many succulents (Michener and Lajtha, 2007). Distinctions of the three categories is facilitated by the fact that each has a definite $\delta^{13}C$ ‰ signature range: C_3 plants = $\delta^{13}C$ -32 to -25; CAM plants= $\delta^{13}C$ - 23 to -18; C_4 plants = $\delta^{13}C$ -16 to -9 (Ostrom et al., 1997; Phillips et al., 2005; Ferger et al., 2013). Therefore in overall, a combined analysis of $\delta^{13}C$ and $\delta^{15}N$ makes it possible to qualitatively link consumers to their food resource options and also determine their trophic positions. SIA as a technique is therefore more robust, accurate and more time-integrated than many classical field ecological methods in trophic studies.

In this study I used analyses of $\delta^{13}C$ and $\delta^{15}N$ to assess how farming systems and cropping methods influence trophic linkages between predacious and herbivorous arthropods on small-scale maize-fields. My specific aim was to identify farming and cropping system combination options that maximize natural suppression of maize-field arthropod herbivores by their natural enemies. I established trophic linkages of an array of arthropod primary consumers to their maize and other basal plant food sources in order to evaluate relative contribution of each food source to consumer diets, and compared between organic and conventional maize farms on the one hand and maize inter-cropped with legume crops versus mono-cropped maize-fields on the other. My expectation was that on organically managed farms, particularly where maize is inter-cropped with legumes, herbivore-to-maize trophic linkages would be lower due to wider plant food options available to herbivores, in contrast to mono-cropped maize under conventional farming systems. I expected also that for the same reason of higher habitat complexity inherent under inter-cropped maize, there would be higher overall trophic linkages between herbivorous arthropods and their arthropod natural enemies, implying higher biocontrol potential here as opposed to maize mono-cop systems.

Although organic farming systems are recognized to be consistent with more structurally complex habitat forms, capable of supporting higher herbivore de-predation by their arthropod natural enemies as compared to conventional farming (Letourneau and Goldstein, 2001; Macfadyen et al., 2009; Norton et al., 2009), it is not always clear how such benefits are influenced by variations in cropping systems within the 'organic' framework. The study addresses this gap and additionally provides insight into how habitat management affects interaction between a wide array of maize-field predacious arthropods and their herbivorous arthropod prey. Maize is important in this study since it the most popular staple crop in most sub-Saharan African countries and is therefore strategically very important for the continent's food security.

3.3 Materials and methods

3.3.1 Study area

I carried out the study in Kakamega County in western Kenya, across 16 small-holder maize fields (Fig. 3.1) selected within a mid-altitude landscape characterised by a high human population density and largely subsistence rural agriculture involving mainly staple crops such as maize, semi-annual legumes, tubers and vegetables as well as livestock rearing (Garcia et al., 2009). The maize grown by farmers is non genetically-modified (non-Bt maize) and as the leading staple grain crop in Kenya and the East African regions, it is grown by nearly every rural household. The mean annual rainfall ranges between approximately 1,200 and 2,000 mm with bi-modally distributed peaks, an intensive long one between March and May and a shorter one from August/September to October/November, and most farmers grow maize in both these rainy seasons.

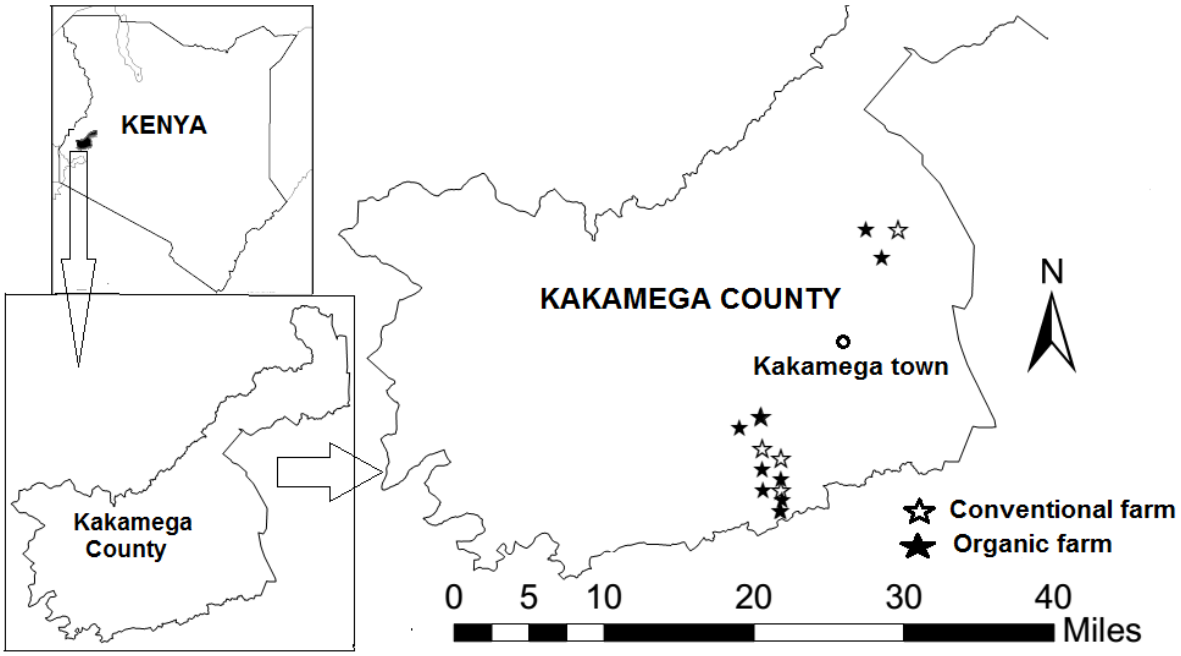

Fig. 3.1. Area where the study was conducted, indicating the locations of study farms.

3.3.2 Farm characterization and selection

I based by farm selection on three topological criteria: 1) presence of non-genetically modified maize crop; 2) cropping system i.e. whole-farm maize monoculture vs maize planted with another crop; 3) farming system i.e. organically managed vs conventionally managed; 4) Absence or non-proximity to any C_4 crop other than maize such as sugar-cane field. Thus 15 farms (9 organic and 6 conventional) were selected, and among these were also 9 farms in which maize was inter-cropped with legume crops (mainly beans) and 6 farms in which maize was mono-cropped. Inter-farm distances were maintained at between 500 – 600 m so as to maintain similarity in general

abiotic characteristics and concurrently ensure sampling independence by minimizing possible effects of inter-farm dispersal of the more mobile arthropods (Beecher et al., 2002).

Organic farmers in the western Kenya region use a range of field management methods including application of farmyard manure rather than inorganic chemical nutrients for soil improvement; mixed or rotational cropping; multiple crop cover types; partial fallowing once in a while; maintaining some length of live indigenous hedgerows; as well as some stand of woodlots for domestic fuelwood use for timber. The system is largely adopted at the individual local scale as it is not officially regulated, and most farmers use it either as a way of minimizing cost of agricultural production or as a form of agronomic diversification, making it a form of small-scale intensification. Conversely, conventional farming at the small-scale involves use of synthetic fertilizers to plant crops with follow-up applications around crop root after each of two weeding periods; total field tillage at each planting period; planting of pre-inoculated seeds; occasional insecticide spraying against insect herbivorous arthropod consumers; no crop rotation; occasional inter-cropping and often no maintenance of semi-natural margins. However, some conventional farmers at times also rest their fields after 3-4 consecutive years of tillage, or may occasionally make use of farmyard manure when they are unable to afford commercial farm inputs.

3.3.3 Field protocol

I undertook sampling at 3 crop stages each during the short-rainy season and the long-rain season (see above section for seasons). The crop stages were: early crop (from germination to first weeding), mid-crop (from second weeding through flowering to cob formation) and at mature-crop (from cob hardening to harvesting). For isotope analysis, I collected 4 plant samples from: target C_4 plant (maize); C_3 crop plants (legumes, typically beans, inter-cropped with maize (hereafter 'legumes IWM'); C_3 non-crop plants (plants from field-margin and from hedgerow). Immediately after collection samples were sealed to reduce moisture loss or air contamination, labelled and sent to the laboratory.

I sampled arthropods twice during short-rain and thrice during long-rain crop seasons. Samples were collected using both standard sweep nets (making 100 sweeps along transects) and pitfall traps, comprising standard 70 mm diameter and 120mm high plastic cups inserted straight upright and flush with ground surface, and filled to one-third with 25% sodium chloride solution for preservation and maintenance of isotopic integrity (Florencio, et al., 2011). With conical plastic rain shields propped above each trap (Brown and Mathews, 2016), I placed 4 replicates randomly along a diagonal line running across each maize-field. Along such diagonal lines, the traps were spaced at distance intervals that depended on maize-field size and they were collected after 3 days but discarded samples in case of too much flooding from rain, and re-set such traps. Care was taken to set the traps as far from the farm's edges' as possible so as to minimize effect of grass food sources that often have isotope signatures comparable to that of maize and are both consumed

by some herbivores (Schweizer et al., 1999; Hobson, 1991; Botha et al., 2017). To supplement sweep-netting and pitfall trapping, arthropods sampled on maize plants using actual pick search-and-pick on leaves, stems, flowers and cobs of cops using forceps, on the all maize plants along every 10th row of each field. At trap collection, I transferred the samples into zip-lock bags and froze them in ice-blocks and sent them to the laboratory (Girard et al., 2011).

In the laboratory, I sorted the plant and arthropod samples and identified arthropods into species and morpho species (Samways et al., 2010). I pooled identified arthropods into two trophic guilds as either primary consumers (herbivores) or secondary consumers (predators). The further pooled predators into 6 sub-pools namely spiders, predacious beetles, predacious bugs, ants, wasps, and earwigs. Similarly, herbivorous arthropods were sub-pooled into phytophagous beetles, phytophagous bugs, lepidopteran larvae, and grasshoppers-and-crickets. For plant samples, the groups were maize (as C_4 plant), beans (legumes IWM as C_3 crops) and non-crop marginal plants (as non-crop C_3). I then oven-dried the sorted and grouped plant and arthropod samples to constant mass before grinding them to fine powder, sub-sampling each group to around 5 mg and finally packing into tinfoil capsules and sending for isotope analysis (Ferger et al., 2013).

3.3.4 Isotopic analyses

I sent the plant and arthropod samples to the Isotope Laboratory of the iThemaba Environmental LABS in Johannesburg, South Africa for analysis of $\delta^{13}C$ and $\delta^{15}N$ isotopes. Analyses were accomplished on a Flash HT Plus elemental analyzer coupled to a Delta V Advantage isotope ratio mass spectrometer by a ConFloIV interface (ThermoFisher, Bremen, Germany) as described in Oelbermann and Scheu (2010). The $\delta^{13}C$ and $\delta^{15}N$ values were expressed as fractions of international reference standards Vienna Pee Dee Belemnite and air, respectively (Post, 2002). The difference (δ) in isotopic ratio between the sample and standards was calculated as: $\delta^{n}X = [(R_{sample}/R_{standard} - 1)]*1000$ where $\delta^{13}X$ is the parts per thousand difference (‰) between the ^{n}X isotope in the sample and that in the standard; R_{sample} is the ratio of heavier to the lighter isotope of the element carbon or nitrogen, and, $R_{standard}$ = the ratio of the heavier to the lighter isotope in the standard (Post, 2002; Fry, 2006).

3.3.5 Data analyses

From the SIA results, I used Bayesian Mixing Model (BMM) method in the stable isotope analysis in the R siar v. 4 package Library (Erhardt and Bedhart, 2013; R Core Team, 2013), to establish a baseline iso-scape of basal food source signatures. Subsequently, I used a multi-source BMM model to establish trophic linkages of the various consumers to the basal iso-scape through their intermediary food sources or prey (Ogden et al., 2005; Girard and Baril, 2011), incorporating

appropriate trophic enrichment factors (TEF). TEFs represent average (Mean±SD) incremental turnover values by which stable isotopic signatures change from food source to consumer tissues up the food chain during the process of metabolic fractionation, (Phillips and Gregg, 2003; Fry, 2006). The BMM functions on the basis that constructing a $\delta^{15}N$ / $\delta^{13}C$ food sources bi-plot creates a food source iso-space polygon that delineates $\delta^{15}N$ and $\delta^{13}C$ qualitatively and quantitatively for each consumer (Bond and Jones, 2009). The TEFs that I applied for herbivorous arthropod consumers were averages according to reviews by Spence and Rosenheim (2005) and for predacious arthropod consumers, averages arising from review for terrestrial invertebrates by Caut et al. (2009) and Ferger et al. (2013). The models wer run for each trophic level separately so as o minimize statistical errors that might arise from multiple-source mixing (Christensen and Moore 2009). Subsequently, I evaluated relative contribution of maize (RCM) and the other plant food sources to the diets of consumers (herbivorous and predacious arthropod groups) (Ogden et al., 2005; Erhadt and Bedrick, 2013). This enabled determination of the extent to which arthropod consumer diets might be traced back to maize as a food source (Phillips and Gregg, 2003; Phillips et al., 2005).

To further underpin predator linkages to maize as a food carbon source, I again ran BMM for $\delta^{13}C$ and $\delta^{15}N$ signatures but this time with predacious arthropod taxa as consumers and arthropod herbivores as food sources. This enabled me to quantify relative proportions of the range of herbivorous arthropod consumer groups to predator diets, and consequently rank the various natural predacious arthropod groups by food source carbon pathway, and therefore identification of potential priority predator groups to be targeted in herbivore suppression management efforts.

I then tested effects of farming systems and cropping methods or combination scenarios, on RCM to the various consumer's diets using generalized linear mixed models (GLMM) in R with the *nlme* package (R Core Team, 2017). I fitted the models using the binomial error distribution with logit link function (Bolker et al., 2009) and based model selection on the least Akaike Information Criterion value. Farming system and cropping methiod were the fixed factors while farm location was a random factor. The models were run per feeding guild.

3.4 Results

Based on the relative contribution of the various basal plant food source options to arthropod consumer diets, the majority of arthropod consumers showed stronger trophic linkages to crops than to non-crops. In the case of maize, ants (Hymenoptera, Formicidae) were the predators with the highest proportions of maize carbon within the organic, conventional and inter-cropped fields, while Earwigs (Dermaptera) had high maize carbon under conventional and intercropping systems, and wasps (Hymenoptera) high maize carbon under mono-cropping (Table 3.1; Fig. 3.2).

Predacious beetles (Coleoptera) had the least trophically linked to maize (Table 3.1; Fig. 3.2). Among herbivores, lepidopterans incorporated the highest proportion of maize carbon in their diet followed by phytophagous beetles (Hemiptera) see Fig. 3.2.

Table 3.1. Ranking of herbivorous and predacious arthropod consumers across farming systems and cropping methods based on relative contribution of maize (RCM) to their diets. RCM is determined as proportion contribution of maize out of all three food source options. P=predator; H=herbivore

Consumers	Organic farms	Conventional farms	Inter-cropped maize	Mono-cropped maize	Mean	Role rank
Spiders (P)	0.42	0.34	0.35	0.29	0.35	5
Predacious beetles (P)	0.33	0.36	0.32	0.31	0.33	4
Predacious bugs (P)	0.40	0.34	0.40	0.36	0.38	2
Ants (P)	0.46	0.42	0.46	0.36	0.43	1
Wasps (P)	0.34	0.36	0.38	0.43	0.38	3
Earwigs (P)	0.38	0.60	0.42	0.38	0.43	1
Phytophagous beetles (H)	0.22	0.08	0.18	0.34	0.21	4
Phytophagous bugs (H)	0.32	0.40	0.22	0.32	0.32	2
Caterpillars (H)	0.22	0.46	0.32	0.42	0.36	1
Grasshoppers and Crickets (H)	0.28	0.36	0.32	0.32	0.31	3

Wasps (Hymenoptera) had the closest linkages to legumes IWM followed by predacious beetles (Coleoptera) and ants while earwigs had the weakest predatory linkage to legumes IWM (Fig 3.2). For herbivory, apart from their leading herbivorous linkage to maize, lepidoptera also had the highest herbivory carbon from legumes IWM, followed by phytophagous bugs (Fig. 3.2). In the case of carbon derived from field margin plants, the closest-linked predators were spiders (almost as much as from maize) followed by earwigs and predacious beetles while the rest of the predators derived almost no food from these plants. Phytophagous beetles were the only herbivorous consumers deriving any notable amount of carbon from marginal plants zone (Fig. 3.2).

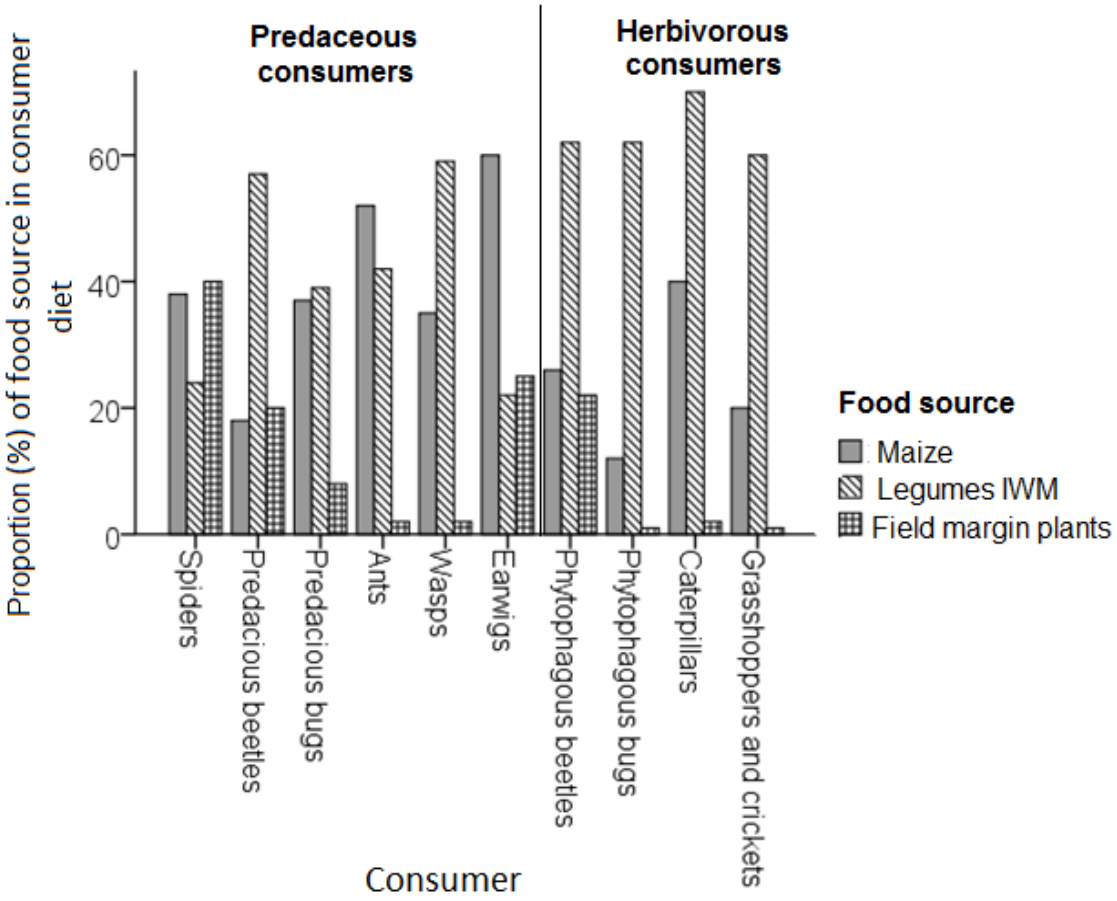

Fig. 3.2 Comparison of relative importance of the three plant food sources in diets of the various predacious and herbivorous consumers across all farms. The importance of food sources were calculated as respective relative proportion of all food sources consumed.

Considering the roles of farming systems and cropping methods on maize contribution to consumer diets (RCM), predators showed significantly stronger linkage to maize carbon under maize inter-cropped with legume (χ^2=1.25; p=0.021) while herbivores showed a higher linkage to maize under mono-cropped maize (χ^2=2.48; p=0.013) see Table 3.2; Fig 3.3. However, RCM did not significantly differ for either guild between organic and conventional farming systems. Similarly, there was no indication that trophic linkage of either guild towards maize carbon would significantly differ in any way between the ecologically most ideal (inter-cropped-organic) versus the least ecologically ideal (mono-cropped conventional) maize systems (Table 3.2).

Table 3.2 General Linear Mixed Model (GLMM) test results of effect of farming systems and cropping methods on relative contribution of maize (RCM) to arthropod consumer diets. Contrasted farming mix scenarios refer to the two options for combining farming systems with cropping methods namely, the most ecologically ideal (inter-cropped-organic fields) versus the least ecologically ideal (mono-cropped conventional fields). Test significance $p<0.05$ and significant values in bold face.

Consumer type	Variables (Farming type)	Coefficient estimate	df	*p*
Predators	Farming system	0.390	4	0.204
	Cropping method	2.113	4	**0.013**
	Contrasted farming mix scenarios	-0.066	8	0.424
Herbivores	Farming system	0.103	4	0.322
	Cropping method	1.981	4	**0.021**
	Contrasted farming mix scenarios	1.981	4	**0.021**

Fig. 3.3. Bar graphs showing comparison of relative contribution of maize RCM to diets of predaceous arthropods and herbivorous arthropods between inter-cropped and mono-cropped maize fields. Error bars represent standard deviations at 95% confidence.

Results of tests linking predacious arthropods to basal plant food carbon sources through their herbivore prey showed that spiders incorporated carbon from every herbivore except

phytophagous beetles while predacious beetles mainly fed on phytophagous beetles and moth larvae. Predacious bugs were the most indiscriminate predators, feeding on all herbivorous prey food sources (Fig. 3.4) while ants tended to avoid phytophagous bugs. Wasps preferred lepidoptera prey and phytophagous beetles but avoided phytophagous bugs while earwigs fed predominantly on phytophagous beetles, taking only less than 10 % of the most significant potential maize and legume arthropod consumers, lepidoptera (Fig. 3.4).

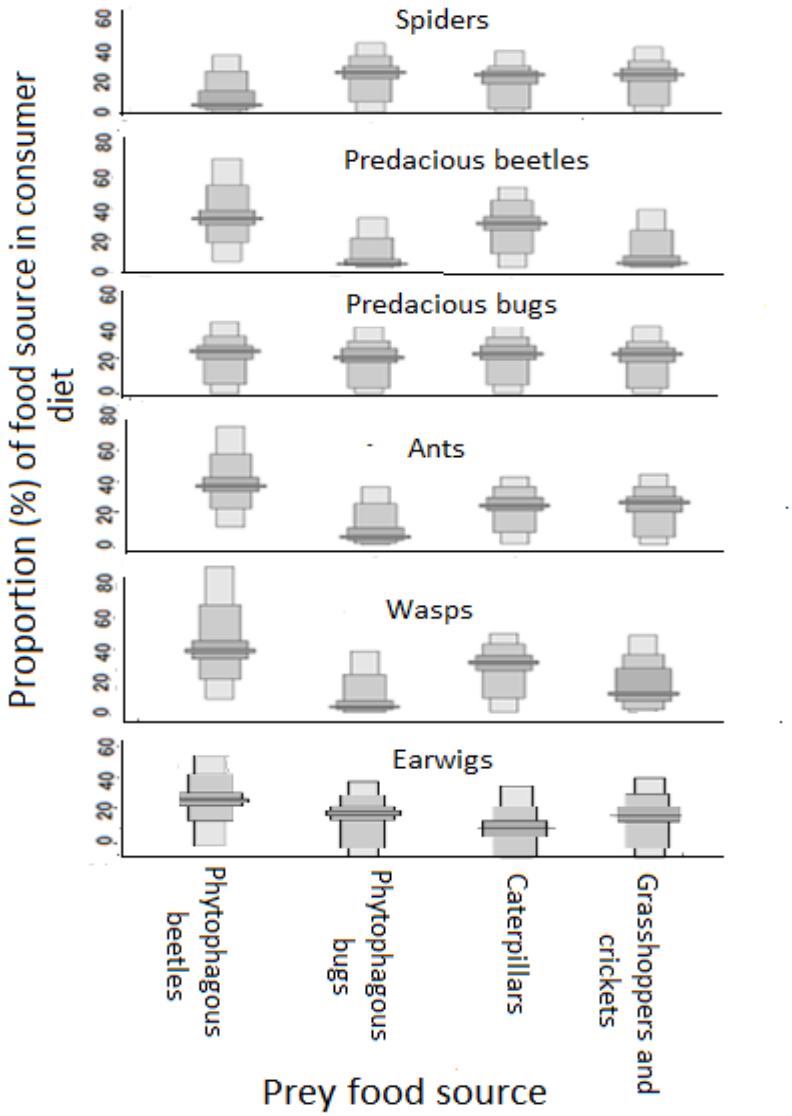

Fig. 3.4. Proportion by source plot of relative contribution of herbivore groups to predacious arthropod diets. The plot bars indicate 5 %, 25 %, 75 % and 95 % confidence estimates for the percent contributions to consumer diets.

3.5 Discussion

Ants emerged overall as the best potential arthropod herbivore suppressors across the maize-fields, a fact that owes to several complimentary aspects of their ecology. They are free dispersers that are generally ubiquitous in almost all microhabitats across the farmland, from the arboreal, ground surface to subterranean, and thus able to exploit prey resources in all these spaces (Landis et al., 2000). They are also active throughout crop growth stages and occur at high densities with wide dispersal abilities, features that do not characterize most of the other predators. As observed by Landis et al. (2000) these qualities, in addition to ants'' constantly itinerant and social hunting habits, make them more successful predators than most of their conspecific competitors.

Furthermore, both ants and wasps were able to derive their dietic carbon from both maize and legumes IWM, however ants were more trophically linked to maize because they consumed a wide range of herbivore prey through which they incorporated proportionately more maize carbon while wasps incorporated more legume carbon, relying more on lepidoptera that were more abundant on legumes IWM than on maize. Predacious bugs also appeared to exploit prey from maize and legumes, and additionally consumed prey from marginal vegetation, though in smaller amounts than maize and legumes. This reflects a somewhat lower dependence by predacious bugs on crop-field prey than was the case for wasps. Predacious beetles, dominated by ground beetles and ladybirds, primarily exploited herbivorous prey on legumes which points to the near-ground surface microhabitat that is shared by both these predators, prey and legume crops. Thus, based on the relative proportion of food source carbon in their diets, wasps and predacious beetles most efficient suppressors of legume arthropod consumers.

However, of all predacious and herbivorous consumers, only spiders appeared to derive equally substantial proportions of their dietic carbon from both the field crops and on field margin vegetation. All the other consumers derived only less than 30% of their carbon from field margin vegetation. This may be explained from two perspectives. On the one hand, for herbivorous consumers, non-crop vegetation may be considered to be of comparatively lower nutritional value as a subsequence of which, for predators also, the marginal vegetation stratum is less attractive because of lower abundance or nutritional value of herbivorous prey from there. However, this is at variance with Rusch et al. (2010) and Gaigher et al. (2015) who observed unequivocally high abundance and diversity of parasitoids in remnant vegetation around agricultural matrices. The contrast of these findings suggest that such semi-natural areas are probably of primary important to predators as refuges or breeding grounds rather than as foraging grounds. On the other hand, for the liberal-feeder spiders, the bet-hedging predatory tendency, often also characterized by inhabiting multi-habitat edges (Clough et al., 2005), demonstrates trophic resilience and functional

plasticity on the spatial and temporal scales (i.e. regardless of access to crop-related carbon). As a matter of fact, Schmidt et al. (2005) noted enhanced spider densities under a mixture of crop and non-crop plants and that the resultant motivation to shuttle between these two habitat types makes them efficient in controlling abundances of aphids across agricultural landscapes.

The heavier reliance by all arthropod consumers on crop food sources as compared to non-crops suggests that occasional fallowing crop-fields may be useful in breaking reproductive cycles for some arthropod herbivore consumer groups, or for preventing their population build-ups to high infestation levels (Song and Swinton, 2009). There was substantial carbon derived by spiders and predacious beetles from both maize and marginal plants, and by wasps from both maize and legumes IWM. This is significant in two ways: firstly, it reaffirms the potential benefit to maize when it is inter-cropped with leguminous crops, in attracting wasps to predate upon maize and legume herbivore consumers. Secondly, leaving semi-natural or uncultivated strips on field edges helps to attract such liberal predators as spiders and ground beetle for maximal and whole-farm integrated pest management (Gibson et al., 2007). Maisonhaute et al. (2010) observed that semi-natural strips or margins either singly or together with farm-level vegetation heterogeneity also enhances diversity and abundance of predacious beetles which the present study has demonstrated to be potentially instrumental in suppressing herbivorous consumers of legume crops. Olufemi et al. (2001) further reported the specific role of inter-cropping maize with cowpeas in facilitating a reduction in infestation of cowpeas by pod-sucking bugs. Studies by Khan et al. (2006) and Cook et al. (2007) also have demonstrated that inter-cropping maize with *Desmodium sp.* as a companion crop, can considerably reduce infestation of maize by the stem borer *Busseola fusca*. Similarly, a review of several studies by Sekamatte et al. (2003) demonstrated that inter-cropping maize with beans or groundnuts not only reduces maize damage by termites (Termitiddae, Letreille, Blattodea) but can also lead to increase in overall maize yields.

Earwigs' high trophic linkage to maize as a food source essentially demonstrates to a large extent that they are significant beneficial predatory agents in regulating populations of maize herbivorous arthropod consumers. However, based on the combined proportion of trophic carbon from all three plant food sources analysed, though earwigs may significantly suppress maize arthropod consumers, they are potentially less efficient regulators at the whole field-wide scale when compared to spiders which derived carbon from all three sources, or to ants, which obtained substantial proportions of carbon from both maize and legumes IWM. Secondly, as generalist feeders with some species being omnivorous consumers (Dib et al., 2011; Romeu-Dalmau et al., 2012a) earwigs may be considered to be less prominent as natural enemies of maize consumers, when compared to the other non-omnivorous predators.. Furthermore the high contribution of maize to earwig diet carbon may additionally emanate from decomposing maize tissue in the soil

since earwigs are also known to be supplemental detritus feeders (Romeu-Dalmau et al., 2012b) and as such may derive maize carbon without direct contact with maize herbivore consumers. Thirdly, earwigs are potentially less effective as predators across the landscape because unlike ants and spiders, they have more localized distributions. Finally, earwigs, unlike spiders and ants, do not occur during all crop growth stages, starting to appear prominently only from around the flowering stage, before which the crops may be at their most vulnerable.

From the observed relative importance of the food sources to arthropod herbivore diets, two main inferences may be made. Firstly, since lepidopterans derived proportionately more of their carbon food from legumes IWM than from maize itself, this group did not present the greatest threat to maize as would be expected. Secondly, the closer trophic affinity of phytophagous beetles, phytophagous bugs and Orthoptera towards legumes IWM rather than towards maize itself (Fig. 3.2) confirms findings by Khan et al. (2001), by Gibson et al. (2007) and by Letourneau et al. (2009) that inter-cropping maize with legumes may provide a buffer to maize against herbivory from these consumer groups.

From the results of predator trophic linkage to plant carbon sources through their herbivore prey, it is clear that field management strategies aiming at minimizing impact of the most significant maize herbivorous consumer group (lepidoptera) should prioritize conservation of spiders, predacious bugs and ants because these predators had the highest lepidoptera-derived carbon in their diets. However, ants appeared limited in their capacity to obtain dietic carbon from phytophagous bugs such as corn-root aphids *Aphis middletonii, Thomas (Hemiptera, Aphididae*) or corn leaf aphids (*Aphis sp.*). This limitation can be explained from the often reported ant-aphid symbiotic relationship where ants derive honey dew produced by the bugs (Buckley, 1991; Young et al., 1997; Cranshaw and Redak., 2013). Therefore biocontrol measures for reducing impact of aphids across maize-field should not necessarily incorporate conservation of ants. Neither should it prioritize predacious beetles especially ladybirds because these also had limited impacts on aphids, as was also reported by Pinol et al. (2009) from studies in a citrus grove. Kindlmann et al. (2005) added that the inability of ladybirds to control aphid populations stems from the generation time ratio theory (GTR) which holds that long-lived arthropod predators such as coccinellids are ineffective regulators of short-lived prey such as leaf aphids.

On the other hand, measures for biocontrolling infestation of lepidoptera alone should focus on attracting any or all of the predators (though earwigs consumed the least of these) while predacious beetles would be ineffective against biocontrolling plant sap suckers (aphids, leafhoppers, plant-hoppers, scale bugs). The beetles (ground beetles and ladybirds) would, however, be very efficient against lepidopteran larvae and phytophagous beetles) particularly on legume crops. Similarly, wasps alone have limited capacity due to their low impact on aphids,

grasshoppers and crickets, but would efficiently suppress moth larvae (lepidoptera) and phytophagous beetles. Earwigs would most effectively control phytophagous beetles and to a lesser extent also regulate phytophagous bugs, but would be comparatively poorer than other predators in suppressing lepidopteran consumers.

The only predator incorporating maize carbon from the full suite of the arthropod herbivore consumers studied, would be predacious bugs as they feed on at least each of the herbivores, even though they achieve this in much smaller proportions compared to the other predators. Spiders would be the second best overall alternative except that they showed relatively low capacity to derive dietic carbon through phytophagous beetles. Due to such limitations, an overall effective scheme to manage herbivorous arthropod consumers would require a range of habitat management systems that supports aggregation of several rather than one predator group because, as reported by Rutledge et al. (2004), the most sustainable impact of an arthropod herbivore biocontrol measure depends on the collective role of a range of enemies, particularly in preventing outbreaks.

Finally, as an empirical guide to the field cultural practices aimed at minimizing costs to the farmer in relation to managing abundance of maize-field arthropod herbivores, the best results would be obtained by either inter-cropping maize with any variety of legume crops, or increasing landscape heterogeneity comprising of a heterogenous mix of different legume or cover-crop matrices interspersed with maize-fields, and maintaining strips of semi-natural field margins and hedgerows. This is because conventional farming systems where maize is mono-cropped and planted within and simplified homogeneous landscape would not only be the most expensive but also the least rewarding for purposes of naturally regulating arthropod herbivores.

3.5.1 Conclusion

Through the results of this study, I have demonstrated four main points. First, inter-cropping maize with legume crops offers the best potential for supporting protection of both crop types through a boost in the trophic linkage between herbivore consumers and their predacious natural enemies. Secondly, most predacious arthropod groups have demonstrable preference or affinity for herbivorous prey that feed on crops rather than on non-crop and this helps in narrowing down the range of habitat management options needed to optimize herbivore regulation. Thirdly, overall effectiveness of maize-field herbivore suppression requires field management techniques that conserve multiple species or a range of natural enemy groups rather than any single one because the most sustainable measure for arthropod herbivore biocontrol depends on the collective role of predatory agents, particularly to prevent pest outbreaks (Letourneau et al. 2009; Wolts et al. 2012). Finally, I have managed to not only role-rank the roles of predacious arthropod groups in suppressing herbivorous consumers of various plants in maize-fields but also distinguish the

relative suppression efficiencies or potential of such predator groups at different functional or spatial scales: earwigs and predacious beetles at single-crop level, ants and wasps at multi-crop level, but spiders at multi-crop and multi-spatial levels.

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Chapter 4: Role of farm structural features on insectivorous birds' contribution to regulation of arthropod herbivores in maize-fields

4.1 Abstract

Despite their role as predators of many cropland arthropods, little is still known of the contributions that insectivorous birds make to reducing crop damage through the suppression of herbivorous arthropods. We examine the role that farming system, crop cover patterns and structural configurations of maize-field play in influencing the assemblage composition of insectivorous birds and their herbivorous arthropod prey, and we determine how bird exclusion affects crop herbivory levels. Sampling was conducted across nine organic and seven conventional small-scale non-Bt maize farms in western Kenya where we assessed how abundance, diversity and richness of insectivorous birds and herbivorous arthropods vary between mono-cropped and inter-cropped maize. In order to determine the impact of insectivorous birds on crop herbivores, we set up a bird exclusion experiment in six plots, three each in two farms, to assess birds' predation impact by comparing herbivorous arthropod abundance across three bird exclusion treatments in each plot (open, semi closed and closed). Results showed that higher structural heterogeneity supported higher insectivorous bird richness, particularly under organic systems, dense trees, large woodlots and thick hedgerows. Bird abundance further increased with crop diversity but not cropping method, hedgerow type or maize cover *per se*. Conversely, herbivorous arthropod abundance and richness increased on conventional farms and with higher percent maize cover, but were unaffected by cropping methods, tree or hedgerow characteristics. Arthropod prey were more abundant under completely closed compared to open or semi-closed plots, indicating a linkage of insectivorous birds to arthropod herbivore suppression. We demonstrate here the importance of structural heterogeneity, and promote incorporating diverse croplands and on-farm trees on agricultural landscapes to attract insectivorous birds that suppress arthropod herbivores in maize fields.

***Key words**:* Structural configuration; Insectivore; Birds; Avian; Ecosystem service; Landscape ecology

4.2 Introduction

Agricultural expansion at various levels of intensity continues to exert pressure on wildlife habitat throughout the world (Freemark and Kirk, 2001; Tscharntke et al., 2012: Laurence et al., 2014). However, many vertebrate and invertebrate species still inhabit croplands or retain ecological linkages to these ecosystems for purposes of dispersal, foraging or reproduction (Flohre et al.,

2011). The concern with herbivorous arthropods is the role they play as pests or potential pest of agricultural crops, with many species expected to be more abundant in farmlands, more productive and geographically spread as a result of climate change (Thomson et al., 2012; Wheeler and von Braun, 2013). A model projection by Deutsch et al. (2018) estimates that arthropods will consume some 10-25% more cereal crops for every 1°C rise in global temperature. Yet although there is urgent need to increase food production, it is equally important to preserve vertebrate and invertebrate biodiversity on farmlands, especially for taxa that are beneficial to crop production through pollination, seed dispersal or suppressing pests through predation (Altieri, 1999; Scherr and McNeely, 2007; Letourneau et al., 2009). Such complementary roles provide the greatest potential for sustainable agriculture but require agronomic practices that recognize the positive contributory role of biodiversity. For instance minimizing the use of agro-chemicals against arthropod pests or weeds will benefit many predatory insects and birds that contribute to reduction of foliar and soil invertebrate herbivores. Minimal application of inorganic nutrients also reduces harmful impacts on ground-level life stages of some predacious arthropods (Zehnder et al., 2006; Gomiero et al., 2011).

Organic farming which typically involves limited or no agrochemical use, together withhigh crop diversification, often with strips of semi-natural margins, is associated with higher habitat structural heterogeneity (Norton et al., 2009; Birkhofer et al., 2011; Macfadyen et al., 2011). This higher habitat structural heterogeneity supports complex functional systems through enhancement of local diversity, which in turn may offset the negative ecological effects of intensive land management practices (Tscharntke, et al., 2005). Furthermore, it has been demonstrated that agricultural landscape configuration in the context of connectivity has considerable influence on energy flow patterns and that such spatial connectivity delimits dispersal of mobile consumers and their prey across the landscape (Lindenmayer and Fischer, 2006; Fabian et al., 2013). More spatially connected habitat matrices are thus important in driving predator-prey interactions as they contribute overall to more trophially linked agricultural landscapes (Perfecto et al., 2004; Martin et al., 2009; Sekercioglu, 2012).

Birds, for instance, prefer structurally complex farm landscapes with trees, uncultivated areas or hedges that provide habitat extensions and increased opportunities for foraging, breeding or refuge from predators (Fischer and Lindenmayer, 2002; Munoz-Saez et al., 2017). Insectivorous birds, in particular, are attracted to heterogeneous agricultural landscapes with higher numbers of arthropods (Rocha et al., 2015; Munoz-Saes, et al., 2017) which can in turn increase their contribution to herbivorous arthropod suppression (Van Bael et al., 2008; Philpott et al., 2009; Jedlicka et al., 2011).

However, insectivorous birds are regarded as less important than predatory arthropods in the role of suppressing crop herbivory, with many farmers, particularly in tropical Africa, devoting much more time and resources to bird control than to habitat management that may attract birds (Wenny et al., 2011; Silva-Andare et al., 2016). This is partly because there are relatively few studies in this region to highlighting significant roles of insectivorous birds as agents of herbivore population regulation (Bianchi et al., 2006; Tscharntke et al., 2007; Rusch et al., 2016). Most such studies have been conducted predominantly in the American regions either on coffee fields (Perfecto et al., 2004; Borkhataria, et al., 2006; Johnson et al., 2010) or in intensively grown corn-fields and other row crops (Tremblay et al., 2001; Garfinkel and Johnson, 2015). Nonetheless, Milligan et al. (2016) assessed the role of birds and ants for controlling coffee pests on highland coffee farms in Kenya, and Ndang'ang'a et al. (2013) quantified the contribution of insectivorous birds in controlling pests on kale vegetables *Brassica oleracea acephala* while Guenat (2014) examined the impacts of insectivorous birds, alongside arthropod parasitoids, in controlling kale damaging aphids under different agroforestry systems. Though still few, such studies indicate a growing scientific interest in Africa, to demonstrate birds' important potential in arthropod pest regulation. However, to our knowledge, no studies have been conducted to assess the role of insectivorous birds in reducing arthropod herbivore populations on small scale maize farms in Africa.

Here, we assess how farm-wide land cover features are linked to spatial variations in composition and assemblage of insectivorous birds to maximize their predatory contribution to suppression of herbivorous arthropods in small non-Bt maize fields in western Kenya. To achieve this we looked at the effect of organic and conventional farming with mono-cropped maize or maize inter-cropped in influencing bird and herbivorous arthropod abundance and diversity response to a range of farm configuration features. We also examined the effect of excluding birds from some plots on two farms to test the linkage between insectivorous bird assemblages and herbivorous arthropod abundance under different exclusion treatments. Our expectation was that maize farms with greater overall structural cover complexity provide more niche space to attract higher richness and diversities of insectivorous birds, potentially enhancing their role in reducing arthropod herbivory. Thus, on plots with full access to birds we expected to find the least abundance of herbivorous arthropods.

4.3 Materials and methods

4.3.1 Study area

I conducted this study in western Kenya's County of Kakamega (Fig. 4.1) an area of mid-level altitude *c.* 1600 m above sea level with crop-field matrices, human settlements, small towns and

water courses, with the main crop grown being non Bt maize (Farwig et al., 2008; Laube et al., 2008; Garcia et al., 2009). Average temperature and rainfall are 21.4^{o}C and approximately 1800 mm, respectively, and the long rains peak between March and May while the shorter rains peak around November (Kenya Meteorological Department, 2017).

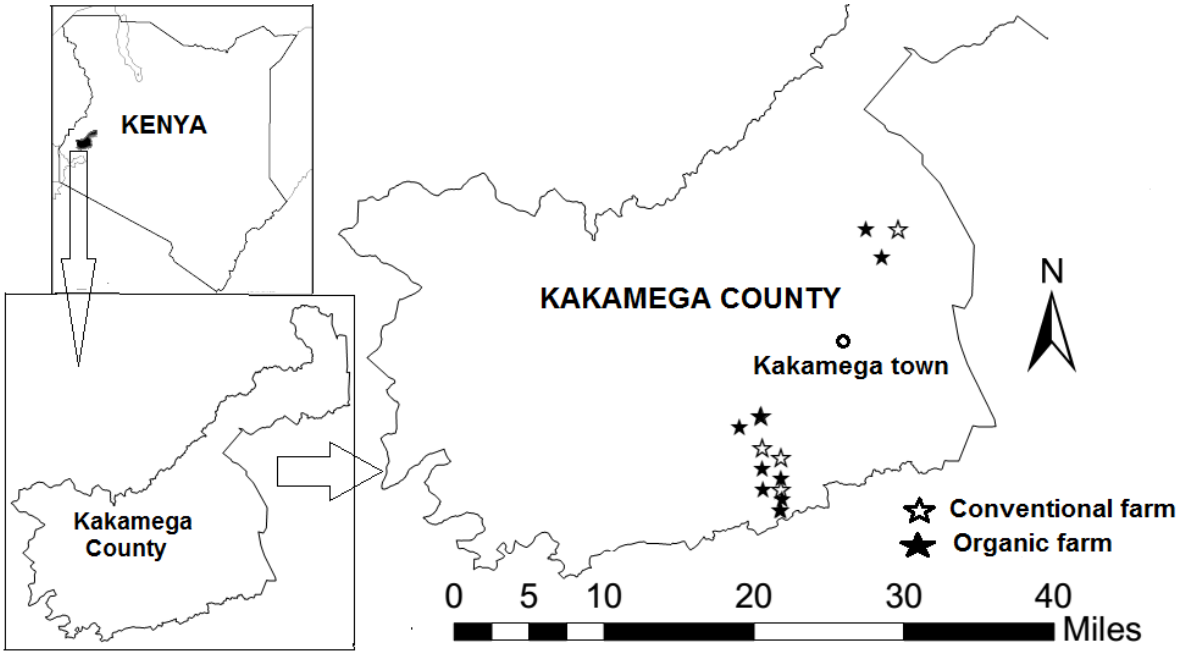

Fig. 4.1. Study area showing locations of study farms by farming system categories.

Organic farming is not practised throughout Kenya and is not regulated under a certification system but farmers using the technique use only organic means of soil fertility improvement especially from animal waste or plant residues, partly due to economic challenges in acquiring inorganic fertilizers and partly for reducing deterioration long-term in soil chemistry (Eden et al., 2017; Silva-Andrade et al., 2016). They also plant multiple crops either through inter-cropping or seasonal rotation and occasionally leave the field to lie fallow, besides maintaining indigenous live hedgerows and woodlots. Maize is often inter-cropped with a variety of pulses (*Fabaceae)* especially beans *Phaseolus vulgaris* or varieties of peas *Pisium sp*. Conversely, those who practice conventional farming tend to have slightly larger crop-fields, predominantly apply inorganic nutrients to fertilize soils in un-rotated crop systems, sometimes inter-cropped; seldom maintain live hedgerows; allow no fallows or uncultivated patches and are less likely to keep livestock (Personal observation). I conducted field sampling during two maize cropping seasons at three cropping stages each between October 2015 and July 2016. The cropping stages were: early-crop (from germination to first weeding), mid-crop (from second weeding through flowering to cob formation) and mature-crop (from cob hardening to harvesting).

4.3.2 Farm selection and habitat sampling

Basing selection criteria on farming system (organic or conventional), cropping method (mono-cropped maize vs maize inter-cropped with legumes), I selected 16 farms (Fig. 1) of which three were mono-cropped organic, six inter-cropped organic, four mono-cropped conventional and three inter-cropped conventional fields. I further characterized the selected farms, which ranged from 0.6 to 9 hectares, as either surrounded by indigenous or exotic live hedgerow, or if there was none, and if the dominant surrounding trees were indigenous or exotic. Independence of samples was ensured by maintaining a minimum of about 500 m inter-farm distance (Beecher et al., 2002).

Farm habitat measures assessed were: maize cover percent; woodlot size; crop diversity (number of crop-field types); hedgerow volume; tree height; tree density. I measured hedgerows using a 100 m tape measure and a metre rule, with heights and lateral widths measured at intervals of 20 m along each farm side, measured hedgerow lengths to the nearest metre but heights and lateral widths to the nearest centimetre. Tree heights were determined using a clinometer. Farming system and cropping methods, hedgerow type and tree type constituted farm biotope factor variables while the other farm habitat measurements were environmental variables.

4.3.3 Bird and arthropod sampling

I surveyed birds using the DISTANCE sampling protocol with line transects (Thomas et al., 2010). While moving at a steady walking pace along a 60 m fixed-width transect centred along the farm's centre line (30 m each side), I made observations using a pair of binoculars and identified birds to species. Surveys were conducted in clear weather between 06:00 and 11:00 to capture the period of maximal activity and detectability (Bibby et al., 2000), recording cluster sizes and perpendicular distances in metres from transect centre by use of a laser range finder (Bibby et al., 2000). I included birds in flight but only when detected to be flying from the front to minimize errors arising from double counting (Bibby et al., 2000). For species moving in flocks, I determined perpendicular distance to the central point of the flock.

I collected arthropod samples using both standard sweep nets and un-baited pitfall traps. consisting of 70 mm diameter and 120 mm high plastic cups inserted in pits with rims flush with ground surface (Pryke and Samways, 2010), and filled to one-third with 25% sodium chloride solution, with conical plastic shields erected above the traps to guard against rain. I randomly placed four replicates along a diagonal line running across the maize-field, with the traps spaced at distance intervals that depended on maize-field size, and collecting the samples after three days, except in case of intensive rain, in which case I discarded such affected samples and reset the traps. To supplement sweep netting and pitfall trapping, arthropods were further sampled using actual

search-and-pick on leaves, stems, flowers and cobs of maize plants using forceps, along every 10th row of each field. I identified the collected arthropods to species or morpho-species (Samways et al., 2010).

In order to test the predatory impact of insectivorous birds on herbivorous arthropods across the maize fields, I set up six cage plots for a bird exclusion experiment within a selected sample of two farms, one organic and the other conventional. The organic and conventional system microclimates within the cages were kept similar to those of the farms in which they were set up. In each of the two selected farms, I set up three such exclusion plots each with a different treatment of bird exclusion: closed (total exclusion of birds), semi-closed (partial exclusion of birds) and open (total access to birds). The exclusion plots consisted of wire cages measuring 3 m long, 3 m wide and 2.5 m high surrounding maize plants without impeding growth. The cage wires were of chicken gauge with mesh sizes of 1.25 x 1.25 cm for closed treatment to exclude all birds but allow arthropod access. Trials showed that small warblers were not excluded with a wire mesh size of 2.5 x 2.5 cm as reported to have been used in a previous study by Ndang'ang'a et al. (2013). For the semi-closed treatment, a grid size of 3.0 x 3.0 cm was used to enable plot access to both arthropods and warbler-size birds and in the open system a marked plot of maize was left open to all birds and all arthropods. I covered the closed and semi-closed treatment plots on all sides including the top, leaving a small entrance for sample collection and replacement. In the cages were mono-cropped maize planted specifically for the experiment, with maize spaced at 0.5 m between rows and 20 cm between plants of each row. I inspected the cages after four days for four weeks during each maize crop stage (early, mid and maturity) for each season of survey. No other crop management action occurred during the four weeks. At inspection, I collected arthropods from every third maize plant on each second row and subsequently identified and counted.

Fig. 4.2. Bird exclusion experiment plots showing the mesh sizes for the three exclusion treatments

4.3.3 Data analyses

I analysed data in R v. 3.4.2 software (R Core Team, 2017) and PRIMER version 6.1 software (Primer-E, 2008). I determined tree densities per hectare, crop diversities as total number of crop varieties, hedgerow volumes in cubic metres. Crop diversity was the total number of different crop-field types and crops planted as a mixture on the same plot were regarded as constituting one crop type. I pooled together arthropod samples from sweep nets and pitfall traps for analysis. For both birds and arthropods, species richness was the cumulative total of all observations for each farm while bird species diversity was determined using Shannon diversity index and arthropod diversity assessed as the inverse of Simpson's dominance index because many arthropod species were represented by very few individuals. Thus I determined arthropod diversity as $D_2 = 1-\lambda$ where D_2 = species diversity and λ = Simpson's dominance index (Magurran, 1988; Pinkus-Rendón, et al., 2000).

I determined bird abundances as densities using the DISTANCE v. 7.1 software (Thomas et al., 2010). Distance sampling caters for both detected and undetected birds by fitting a detection function of relationship between a bird's detectability and its distance from the transect line (Buckland et al., 2001). I grouped birds following nomenclature of Fry and Keith (2004) and the guild assignment system used by Kissling et al. (2012) modified to incorporate omnivorous species. I determined the densities by fitting detection functions for each species but on the global scale (Newson et al., 2008). Thus each farm was treated as a transect within the study area, and samples from all survey periods were pooled for final analyses. Having spatially standardized detection probabilities, I then grouped species into four analytical categories in terms of degree of

commonness. For those species that were encountered at least ten times across all observations and regarded as common, I fitted detection functions for each individually. I clustered the rest into three bands such that those encountered 7-9 times were grouped as 'uncommon', those encountered between 4-6 times I grouped under 'rare' and those encountered 1-3 times I grouped as 'very rare', and one detection function was fitted for each of the three bands. Thus, a total of 23 detection functions were fitted. In each case, I based the detection function model selections on the lowest Akaike Information Criterion (Thomas et al., 2010).

Global fit of detection functions for densities was appropriate because the maize farming landscape represented a standardized habitat type and thus no significant differences in bird detection probabilities were expected (Bibby et al., 2000; Thomas et al., 2010). For flocking species encountered at least thrice during a survey, the cluster size value used in fitting detection function was the average for the total number of their encounters for each farm. This allowed me to minimize errors associable with flock cluster size estimation (Meadows et al., 2012). Majority of the models selected were half-normal with cosine adjustments of order 2 or 3 (Thomas et al., 2010). Subsequently, for each farm, I estimated populations for each species or group, per farm, from the derived global densities such that $P_{Sn} = D_{Sn} * S_F$ where P_{Sn} = population of species *n*; D_{Sn} = global density of species *n*; S_F = farm size.

I also derived a structural heterogeneity index for each farm from a sum value arising from a 1 - 3 score of hedgerow volume value band (3 for the highest); number of crop varieties; a 1-3 score of tree density value band (3 for the highest); a score of 1 or 2 for faming system (2 for organic farming); and score of 1 or 2 for cropping method (2 for inter-cropping). Thus the heterogeneity index was: $HIn = IHV+ICD+ITD+IFs+ICr$, where *HV*, *CD*, *TD*, *Ts* and *Cr* are hedgerow volume, crop diversity, tree density farming system and cropping method, respectively. I used Distance based linear modelling (DistLM) in PRIMER (Primer-E, 2008) to identify farm habitat attributes that explained arthropod and bird diversities and species richness. For birds, I included arthropod species richness and diversities (Shannon or Simpson's Dominance) in the model as additional explanatory variables. DistLM were run on square-root transformed Bray-Curtis similarity matrices of abundance data for birds and arthropods, and on normalized similarity matrices on Euclidean distances for environmental data (McArdle and Anderson 2001). I ran the models stepwise and made selection based on Akaike Information Criterion, and the variables that best explained variations in assemblage similarities were identified at $p<0.05$ from sequential tests.

I further used Generalized Linear Mixed Models (GLMM) in the *nlme* package in R version 3.4.2 (R Core Team, 2017) to assess responses of bird and herbivore abundance, species richness and diversities to farm habitat variables (Bolker et al., 2009). I fitted the models with Poisson error probability distribution and log-likelihood link function for species richness and abundances,

and with binomial error distribution with logit-link function for Shannon and Simpson's dominance indices (Bolker et al., 2009). Farm number was included as a random effect, and I included the other predictor variables (farm biotopes and environment variables) in the model as fixed factors. For bird dependent variables, I included arthropod abundance, richness and diversities as additional independent variables.

I also used the Permutational Multivariate Analysis Of Variance procedure PERMANOVA+ add-on to PRIMER (Primer-E, 2008) to assess farm and temporal factors that significantly explained the abundance similarity patterns of herbivorous arthropods within the insectivorous bird exclusion experimental plots: open, semi-closed and closed, with data from both experimental farms pooled up together (Primer-E, 2008). Such PERMANOVA tests were run with 9999 permutations for main effects of all factors and then with unrestricted permutations for pairwise within-group effects in case of significant factors.

To further assess influence of habitat factors on the bird-arthropod predation linkage I performed analysis of covariance (ANCOVA) to test the combined influence of farming system on bird and herbivorous arthropod aggregations with the goal of potentially modelling for scenarios of maximal impact of birds on arthropod herbivore abundance. To meet assumptions of ANCOVA, the two bird-arthropod dependent variables selected had to be moderately correlated, normally distributed and with variance homogeneity, confirmed using Box's M tests (Nakagawa and Cuthill, 2007). Further, the correlation between the variables in question needed to be negative in order to fit an inverse effect of birds on the herbivorous arthropods. Based on such constraints and conditions, I settled on bird species richness and herbivorous arthropod diversity as the dependent variables, farming system as independent variables and farm size was the fixing covariate since there was a high variation in farm sizes (mean = 3.20±0.66; std dev = 2.71). I used Wilks Lambda value in assessing ANCOVA's overall multivariate response of dependent to independent variables, and I applied the Bonferroni correction to the confidence intervals of adjusted means. Subsequently, I ran separate ANOVA tests to assess univariate effects of the independent and covariate variables on the dependent variables.

4.4 Results

I recorded a cumulative total of 80 insectivorous bird species from 30 families and 78 herbivorous arthropods species or morho species (Appendix 2). In general, there were more insectivorous bird species on organic than on conventional farms while herbivorous arthropods were more abundant on conventional fields (Table 4.1). Insectivorous birds were also more diverse on organic than on conventional farms.

Table 4.1. Insectivorous birds and herbivorous arthropod abundance, species richness and diversities across the farms. Bird abundances were estimated based on densities derived from the globally-fitted detection function across all farms. Species richness represents cumulative number of species observed over the entire study period.

	Insectivorous birds			Herbivorous arthropods		
Farm biotope treatment	Mean density (Per ha)	Species richness	Shannon diversity	Mean abundance per sample	Species richness	Simpson's diversity
Organic farms (N = 9)	32.2±3.8	77	-1.467	56.4.9±6.1	55	0.121
Conventional farms (N = 7)	23.4±2.1	56	-1.128	120.8±4.4	38	0.290
Inter-cropped farms (N = 9)	36.4±2.6	74	-1.287	74.8.5±5.0	50	0.230
Mono-cropped farms (N = 7)	31.0±4.3	63	-1.243	99.5±6.6	45	0.192
Indigenous hedgerows (N = 8)	35.6±2.5	78	-1.243	119.0±11.8	64	0.218
Exotic hedgerows (N = 5)	34.1±3.3	40	-1.272	132.2±18.3	28	0.137
No hedgerows (N = 3)	27.2±7.2	17	-1.123	160.8±.14.3	10	0.134
Indigenous trees dominant (N = 12)	29.9±8.8	74	-1.274	52.3±6.9	66	0.139
Exotic trees dominant (N = 4)	34.4±1.6	47	-1.149	164.9±23.1	26	0.353

PERMANOVA test results showed that farming system influenced assemblage patterns of insectivirous birds with a significant variation in assemblage matrices between organic and conventional farms (Table 4.2). There was also a significantly higher abundance of insectivorous birds on farms with higher densities of exotic as compared to those dominated by indigenous trees (Table 4.2). No farm biotope showed any significant relation to herbivorous arthropod assemblage patterns (Table 4.2).

Table 4.2. PERMANOVA test results showing probability ($p<0.05$) values for effects of farm biotope factors on assemblage of herbivorous arthropod and insectivorous birds. Values in parentheses are corresponding pseudo-F values, and significant effects are in bold face.

Source	Df	Herbivorous arthropods	psedo-F	Insectivorous birds	psedo-F
Farming system	1	0.164	1.384	**0.024**	1.467
Cropping method	1	0.592	0.887	0.838	0.622
Hedgerow type	2	0.217	1.217	0.313	1.141
Dominant tree type	1	0.412	1.065	**0.045**	1.651

From DistLM models, only the proportion of maize cover significantly influenced compositional assemblage similarity of herbivorous arthropods, explaining 80.4% of the variation (Table 4.3). For bird assemblages, hedgerow volume explained 10.1% of assemblage variations in birds overall (Table 4.3). Similarly, for insectivorous bird assemblages, hedgerow volume together with herbivorous arthropod species richness and herbivorous arthropod diversity explained 41.6% of the variation (Table 4.3).

Table 4.3. Results of sequential tests from distance based linear models (DistLM) for significant effects ($p<0.05$) of environmental variables on alpha diversities of herbivorous arthropods and insectivorous birds.

Taxa alpha diversity	Variable	Pseudo-F	p	Proportion (%) explained
Herbivorous arthropods	Percent maize cover	3.351	0.019*	80.4
Birds overall	Hedgerow volume	1.589	0.041*	10.2
Insectivorous birds	Hedgerow volume	1.234	<0.001***	19.3
	Herbivorous arthropod species richness	2.166	0.007**	10.5
	Herbivorous arthropod diversity	2.234	0.038*	11.8

Code: $p>0.05$, *$p\leq0.05$; **$p<0.01$; ***$p<0.001$)

From generalized linear mixed model (GLMM) tests, herbivorous arthropod abundance was affected by farming system and proportion of maize cover, whereby conventional farming and higher maize cover proportion each enhanced herbivorous arthropod abundance (Fig 4.3), species richness and diversity (Table 4.5). Similarly, there were significantly more herbivorous arthropods on farms dominated by exotic trees as compared to those dominated by indigenous tree varieties (Table 4.5).

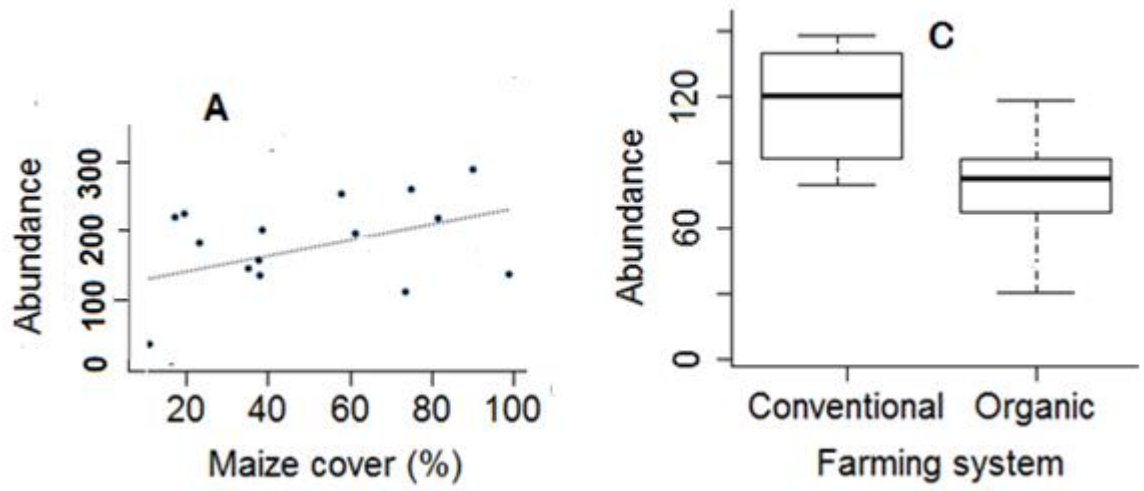

Fig 4.3. Scatterplot of how herbivorous arthropod abundance was influenced by A) proportion of maize cover and B) farming system.

For insectivorous birds on the other hand, there was no significant influence of farming system or cropping methods on abundance but organic farms had higher species richness and diversity (Table 4.4). Higher arthropod herbivore abundance further attracted insectivorous birds in higher aggregations, species richness and diversity (Table 4.4; Fig 4.4). Farm heterogeneity showed an additional positive influence on insectivorous bird species richness but not on insectivorous bird abundance, diversity or herbivorous arthropod compositions (Table 4.4).

Table 4.4. Generalized Linear Mixed Model GLMM) test results for effects of environmental variables and farm biotope factors on measures of composition of insectivorous birds and herbivorous arthropods across the farms, with farm number as random effect. Bird abundances represent population estimates from globally fitted detection function densities; bird diversities represent Shannon diversity indices while arthropod diversities represent the Inverse of Simpson's Dominance Indices. Heterogeneity refers to overall heterogeneity index. Significance level was set at $p<0.05$ and significant effects are in bold face.

	Insectivorous birds			Herbivorous arthropods		
Factor/variable	Abundance	Species richness	Species diversity	Abundance	Species richness	Species diversity
Farming system	0.745	**0.009**	**0.013**	**0.009**	0.110	0.157
Cropping method	0.690	0.297	0.266	0.278	0.318	0.551
Hedgerow type	0.650	0.134	0.127	0.598	0.555	0.224
Dominant tree type	0.447	0.369	0.146	**0.031**	0.227	0.164
Hedgerow volume	**<0.001**	**0.037**	0.096	0.508	0.993	0.190
Maize cover %	0.111	0.444	0.882	**<0.001**	**0.012**	**0.039**
Crop diversity	**0.031**	0.645	0.653	0.146	0.130	0.720
Woodlot size	**0.050**	**0.016**	**0.024**	NA	NA	NA
Tree density	0.918	**0.029**	**0.026**	NA	NA	NA
Mean tree height	0.612	**0.036**	0.056	NA	NA	NA
Heterogeneity index	0.079	**0.050**	0.136	0.264	0.561	0.443
Herbivorous arthropod abundance	**0.041**	**0.041**	**0.044**	NA	NA	NA

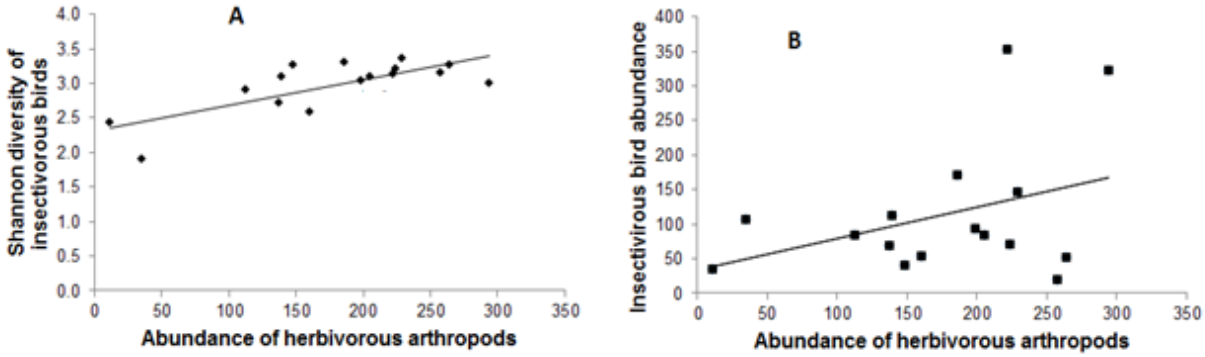

Fig 4.4. Scatterplot of effect of herbivorous arthropod abundance on A) diversity and B) abundance of insectivorous birds.

For birds overall, organic farming enhanced abundance and species richness while type of dominant tree showed no influence (Table 4.5). But of the habitat measure variables, taller trees attracted higher overall bird species richness (Table 4.5). Similarly, overall habitat heterogeneity was important in boosting both abundance and diversity of birds overall (Table 4.5)

Table 4.5. Generalized Linear Mixed Model (GLMM) test results for effects of environmental variables and farm biotope factors on assemblage measures of birds overall across the farms. Bird abundances represent population estimates from globally fitted detection function densities; bird diversities represent Shannon diversity indices while arthropod diversities represent the Inverse of Simpson's Dominance Indices. Heterogeneity refers to overall heterogeneity index. Significant effects are shown in bold face.

Factor/variable	Abundance	Species richness	Species diversity
Farming system	**0.017**	**0.003**	0.813
Cropping method	0.141	0.669	0.993
Hedgerow type	**0.018**	**0.022**	0.860
Tree type	0.538	0.241	0.955
Hedgerow volume	0.494	0.458	0.317
Maize cover %	0.154	**0.046**	0.097
Crop diversity	0.290	0.354	0.655
Woodlot size (ha)	**0.007**	0.319	**0.012**
Tree density (per ha)	0.121	0.928	0.255
Mean tree height	0.196	**0.013**	0.058
Heterogeneity	**0.016**	0.828	**0.035**

PERMANOVA test results showed a significant general main-effect on the three treatment levels (closure, semi-closure and openness) on abundance similarity matrices of herbivorous arthropods across the insectivorous bird exclusion experimental plots (Table 4.6) with closed systems recording the highest abundance of herbivorous arthropods, followed by open and semi-closed systems, respectively (Fig 4.5).

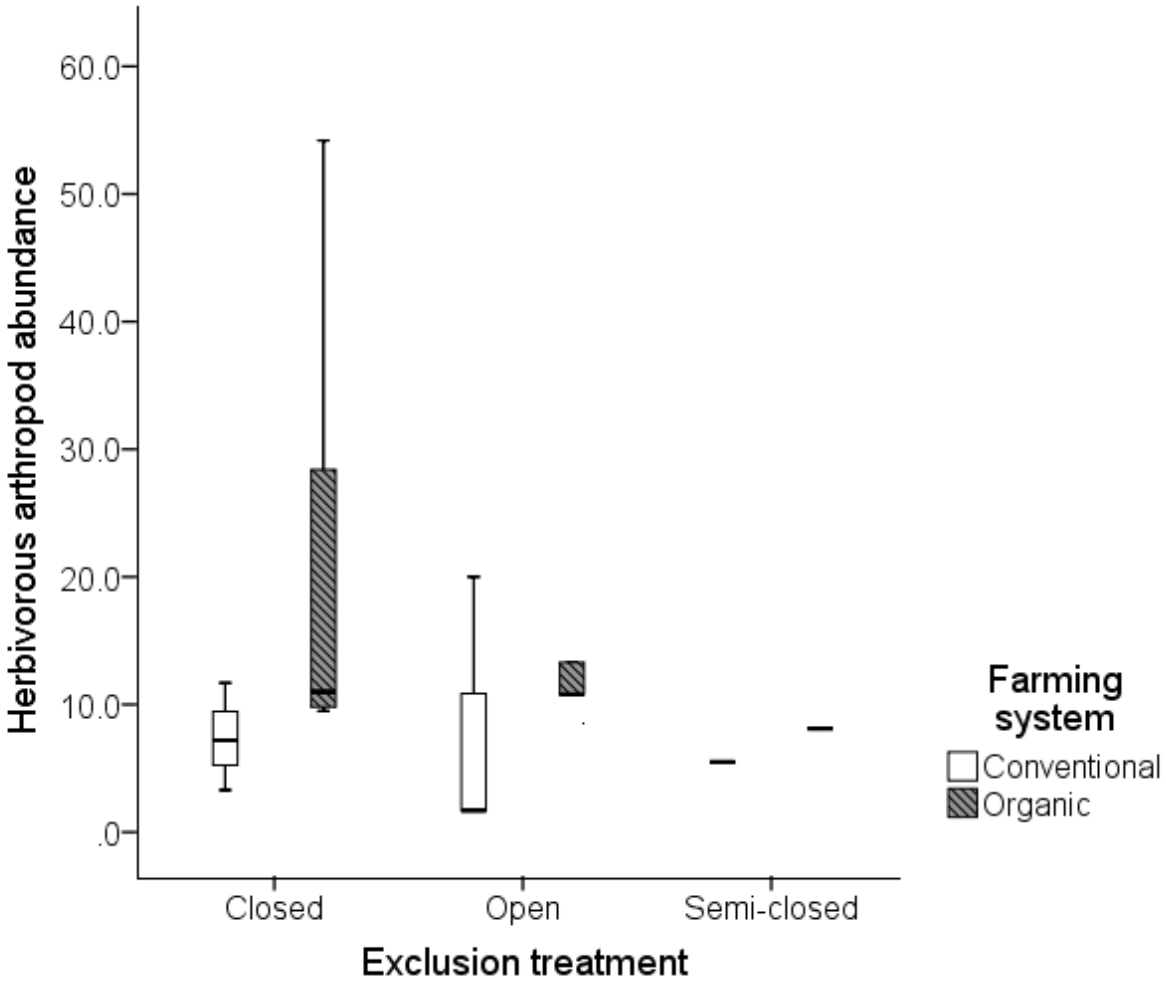

Fig 4.5. Error bars comparing herbivorous arthropod abundance across the three enclosure treatments of the insectivorous bird exclusion experiment. Top and bottom of error bars represent standard errors. Error bars represent standard deviations at 95% confidence.

Subsequent pairwise tests within the closure treatments showed a significant difference between the closed and the open treatments, indicating a significant predatory link of the birds to the arthropods but no difference between closed and semi-closed or between semi-closed and open treatments (Table 4.6).

Table 4.6. PERMANOVA test results for effects of farm factors, treatments and temporal variables on herbivorous arthropod abundance similarities across the insectivorous bird exclusion experiment plots.

Effect	Explanatory variable	df	SS	MS	Statistic	p	Unique permutations
Main	Season	1	308.5	308.51	Ps-F = 0.266	0.893	9948
	Farming system	2	4560.6	2280.3	Ps-F = 1.965	0.081	9936
	Crop stage	2	1922.6	961.31	Ps-F = 0.828	0.585	9943
	Bird exclusion treatment	2	5142.6	2571.3	Ps-F = 2.215	**0.049***	9956
Within-group	Closed vs Open	9	-	-	t = 2.001	**0.009****	9954
	Closed vs Semi-Closed	3	-	-	0.52562	0.859	9941
	Open vs Semi-Closed	4	-	-	0.51637	0.858	9845

Code: P>0.05, *P≤0.05; **P<0.01; Ps-F = Psuedo-F; Significant effects (p<0.05) are in bold.

There was also a significant effect of farming system, with a significantly higher herbivorous arthropod abundance on organic farm exclusion plots compared to plots on conventional farm plots (p = 0.032) . Similarly, crop-stage influenced herbivorous arthropod abundance in the exclusion experiment (p = 0.049) and Tukey post hoc test showed a significant difference between early and middle crop stage (Tukey LSD = 1.991, p = 0.046) though there appeared no differences between early and late crop stage (p = 0.550) or between middle and late stage (p = 0.419). Cropping season did not show any effect on herbivorous arthropod abundance across the exclusion plots.

From the ANCOVA test of bird-arthropod predatory linkage, the multivariate overall test returned a significant effect of farming system on the combined response of insectivorous bird species richness and herbivorous arthropod diversity (Wilks lambda score = 0.490, F = 6.250, p = 0.014, df = 12). For univariate within-groups ANOVA tests, farming system had significant effects on both bird species richness and herbivorous arthropod diversity, with organic farms having higher bird species richness than conventional farms (F = 7.434, $df_{(1,13)}$, p = 0.017) while conventional farms had higher herbivorous arthropod diversity than organic farms (F = 4.795, $df_{(1,13)}$, p = 0.047) (see Table 4.7; Fig 4.6).

Table 4.7. Within-groups univariate test results of Analysis of Covariance of effects of farming system on populations of insectivorous birds and herbivorous arthropod diversity. Farm size was fixed as a covariate.

Dependent Variable	Farming system	Estimated mean	Standard error	95% Confidence Interval	
				Lower Bound	Upper Bound
Insectivorous bird species richness	Conventional	307.432[a]	49.991	197.403	417.461
	Organic	466.204[a]	37.174	384.386	548.023
Herbivorous arthropod Simpson's diversity	Conventional	0.340[a]	0.096	0.130	0.551
	Organic	0.122[a]	0.071	-0.035	0.278

a. Covariates appearing in the model are evaluated at farm size = 2.303

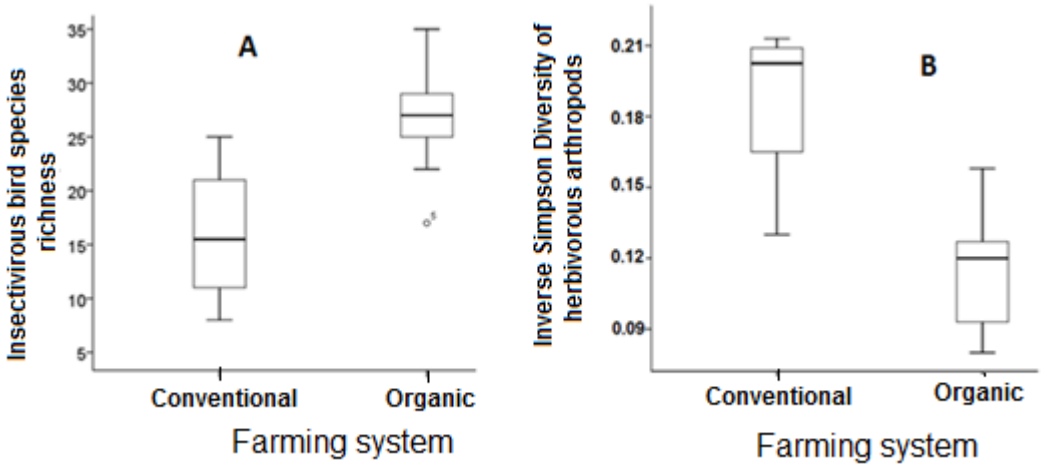

Fig 4.6. Box plots comparing A) insectivorous bird species richness and B) herbivorous arthropod diversities between the farming systems. Diversities are calculated as Inverse of Simpson's Dominance index. The lower and upper segments of the bars represent the second and third quartile group of the distribution, the horizontal bar represents the median of the observed distribution while the bottom and top segments of error bars represent 95% confidence intervals.

4.5 Discussion

Higher species richness and diversity of insectivorous birds on organic compared to conventional farms indicates that organic farming systems generally facilitate habitat structural complexity, which increases niche variability attractive to a wider variety of birds. Imai et al. (2017) found that insectivorous bird species richness responded positively to habitat heterogeneity represented by higher cover of woody vegetation in Tochoku, Japan but unlike in the present study, they observed

the same response for insectivorous bird abundance. On the other hand, Munoz-Saez et al. (2017) attributed increased richness of insectivorous birds to available hedgerow surface area. Organic farming also supports lower dominance amongst insectivorous bird species because their arthropod prey occur in non-clumped distribution under such high habitat complexity conditions ant at higher abundances due to the healthier chemical-free environment of organic systems (Aktar et al., 2009).

Although there was no effect of hedgerow type, whether indigenous or exotic, when hedgerows occurred in thick and voluminous form, they not only enhanced overall field heterogeneity but may also offer nesting habitat for some insectivorous birds, and harbour some arthropod prey to supplement those on actual crop-fields (Borges et al., 2017). As pointed out above, higher overall surface area of hedges was attractive to a wider variety of insectivorous bird species. Apart from foraging opportunities, hedges additionally serve as dispersal corridors to connect natural habitats fragmented by the agricultural landscape (Burel, 1996).

Similarly, a crop-diversified farming field is attractive to large numbers of insectivorous birds because they have a correspondingly wider choice of arthropod herbivore prey that also target a variety of their own crop food sources (Bianchi et al., 2006). This is more so under organic farming systems characterized by patch matrices of different crops and other marginal plants. Therefore, the positive response of bird abundance to crop diversity but not to inter-cropping *per se*, shows that birds perceive structural agronomic systems at a spatial scale wider than the local farm field level (Kellermann et al., 2008). Additionally, herbivorous arthropods, the main attraction to insectivorous birds, were more heavily drawn to farms with higher maize cover proportions regardless of cropping methods, and this over-rode the importance of maize-legume inter-cropping as an attractant factor to insectivorous bird aggregations.

On-farm trees were similarly important in determining insectivorous bird assemblage and compositions. Large woodlot stands, for instance, supported not only higher bird aggregations but also species varieties, underscoring the role of woodlots in expanding the farm-field dispersal habitat to augment the role of hedgerows and reduce bird species dominance. Woodlots also offer roosting sites and refuges from predators or anthropogenic disturbance while also providing additional foraging surfaces (Newmark and Stanley, 2016; Zufiaurre et al., 2017; Personal observation). On-farm trees occurring at higher densities or heights, further served to attract more species and varieties of insectivorous birds, which is consistent with findings of Clough et al. (2009) of higher abundances and richness on more densely wooded regions within cacao agro-forested systems in Indonesia. Trees not only increase insectivorous bird habitat area but also serve as stepping stones for dispersing across large habitat patches in agroecosystems (Fischer and Lindenmayer, 2002). Railsback and Johnson (2014) noted that for insectivorous birds, trees also

provide vantage perches for efficient foraging, while taller trees in particular are important to males as singing posts for territorial defence, mating contacts or safe refuges against terrestrial predators. They added that even in small patches near coffee fields, trees were important in attracting insectivorous birds that predated upon herbivorous arthropod consumers of coffee berries, and that the distribution patterns of trees was unimportant for such birds.

Another strategy that was reported to be successful in some California vineyards was from a study by Jetlicka et al. (2011) who observed improved predation by insectivorous birds on crop herbivores when nest boxes were installed to increase density of cavity-nesting bird species across the fields, which significantly reduced damage to the crops. Such a strategy is worth exploring in tropical regions particularly in view of rapidly declining availability of suitable mature trees for many cavity nesters as a result of natural forest conversion to farmland and settlement (FAO, 2016).

Nevertheless, despite the individual effects of on-farm tree density, woodlot size and hedgerow volume, the influence of overall habitat structural heterogeneity on insectivorous birds was restricted to species richness but not abundance or diversity. This underscores the focal role of structural complexity in expanding niches for a larger range of bird species rather than encouraging large aggregations of dominant species across the agricultural landscape. Alternatively, the role of heterogeneity in supporting insectivorous bird assemblage, and by extension, predation role on arthropod herbivores, may be a function of both habitat complexity superimposed on or mediated by the functional diversity of the birds themselves, as suggested by Barbaro et al. (2017) in their study on an American vineyards, such that narrow ranging species may be more effective in arthropod suppression. This is likely the case because in the present study, high abundance of herbivorous arthropods appeared to attract a higher diversity and richness of insectivorous birds thereby underpinning the close bird-arthropod trophic linkage and role of this linkage as a deterrent to potential herbivore population build-ups (Karp and Daily, 2014).

Conversely, the higher arthropod herbivore abundance on conventional than on organic farms indicates their affinity to structurally simplified habitat systems characterizing most conventional farming systems. This not only concurs with findings by Chaplin-Kramer et al. (2011) that arthropod herbivores have low response to habitat heterogeneity, but also indicates vulnerability of maize monoculture landscapes to the risk of herbivorous arthropod proliferations. Accordingly, arthropod herbivores assemblages were unaffected by heterogeneity elements such as hedgerow volume but instead responded strongly to maize cover proportion, further pointing to maize as important both as a food source and habitat in contrast to hedgerows or other field margin vegetation. Compounded with intensive use of agrochemicals, the habitat simplicity of conventional farms are also associable to reduced populations of herbivores' arthropod natural

enemies (Desneux et al., 2007; Atkar et al., 2009; Bommarco et al., 2011) and this undermines the potential impact of such predators in suppressing crop herbivory. On the other hand, association of exotic trees to increased abundance of herbivorous arthropods, while unexpected, might be explained by the fact that most of the exotic tree species on the farms were *Grevillea rocusta* and *Pinus* sp both of which have high leaf densities, a structural attribute that may provide suitable breeding or refuge habitats. *G. robusta* is particularly favoured by farmers as an agroforestry tree crop in tropical farming regions (Jackson, 2000; Kalingarine et al., 2001).

Higher herbivorous arthropod abundance under bird-excluded plots provided further evidence of the trophic linkage between insectivorous birds and herbivorous arthropod prey. This clearly indicates the role of insectivorous birds as contributors to overall regulation of crop-damaging arthropods. A similar observations of insectivorous bird predation role on crop pests was made by Johnson et al. (2009) and Morrison and Lindell (2012) who respectively reported increased leaf damage and infestation by the coffee berry borer *Hypothenemus hamperi* when insectivorous birds were excluded from accessing coffee trees in Jamaica and also in Guam. On the other hand, the insignificant difference in herbivorous arthropod abundances between open and semi-closed and also between semi-closed and closed treatments suggest that predatory arthropods within the semi-enclosed plots, may have a considerable complimentary role to that of birds in naturally suppressing herbivorous arthropods. In a comparable incident, Tremblay et al. (2001) showed that even though maize herbivorous arthropods occurred at higher densities when maize plots were closed to bird access, shortfalls in net maize yield remained disproportionate to observed herbivore abundance, implying that the shortfall may be accounted for by the impact of predation by arthropod herbivore's natural enemies which, like herbivores, also have access to exclusion cages. This, in itself, may allude to a possible mild trophic cascade by insectivorous birds upon predacious arthropods, when the former includes some species of the latter in its range of prey items under purely open field conditions (Van Bael et al., 2008; Mooney et al., 2010; Mäntylä et al., 2011).

Higher herbivorous arthropod abundance on organic as compared to conventional farms under the enclosure experimental plots, with the highest value at the middle maize-crop stage treatment, suggests four possibilities. Firstly, if insectivorous birds were to be totally excluded from maize-fields, arthropod herbivore populations, particularly specialist maize consumers, may increase rapidly beyond the regulatory capacity of predacious arthropods alone, in spite of increased habitat heterogeneity and healthy environment offered by organic farming. Alternatively, the role of organic farming in mediating arthropod herbivore population regulation via natural suppression is tenable only at spatial levels wider than the enclosure plots, as was

posited by Tscharntke et al. (2005) and Tscharntke et al. (2008). The third possibility is that at the middle stage of maize growth, there is a higher diversity of maize plant parts (leaves, flowers, new cob and stem) to sustain more diverse herbivorous arthropods when compared to other stages, particularly on organic farms. The final possibility is that there is comparatively higher herbivory pressure on the maize crop at the mid stage because it coincides with or immediately succeeds the harvesting time for legume inter-crops which matures earlier than maize (Personal observation), hence many generalist arthropod herbivores previous relying almost exclusively on legume food sources, suddenly make a compulsory diet shift towards maize.

4.5.1 Conclusion

Overall, these findings confirm that organic farming systems maximize the likelihood for insectivorous birds' contribution to herbivorous arthropod abundance regulation across maize-fields because the resultant habitat quality attracts supports higher richness and diversity of the birds. Specifically, structural heterogeneity in maize farms, particularly with on-farm trees under organic farming, attracts diverse bird species, cover diversification and thicker hedgerows enhance aggregations while maintenance of woodlot stands attracts species in both abundance and variety. On the other hand, herbivorous arthropods are predominantly attracted in large numbers by large expanses of maize cover grown on structurally simple farm fields in contrast to predacious arthropods that generally respond positively to habitat complexity, similar to observations by Lichtenberg et al. (2017). Thus conventional and mono-culture farming systems appear more susceptible to risks of more prolific or invasive herbivory since such farm systems are more structurally simplified through intensification, as was shown by Rusch et al. (2016) and such farming systems offer limited niches for higher abundances and varieties of beneficial predacious arthropods or more species of insectivorous birds. Therefore faming maize under field conditions characterized by cover diversification, thick hedgerows and presence of on-farm trees, represents a form of conservation agriculture that is useful in facilitating the role of insectivorous birds' contribution to the ecosystem function of herbivorous arthropod suppression (Sain et al., 2017). The importance of these structural attributes in promoting such herbivore regulation is more pronounced in the case of insectivorous bird species with narrow home rages, whose impact on crop herbivores are therefore more efficient due to more localized, intensive foraging efforts. Further, as the findings by Railsback et al. (2014) showed from studies on coffee farms, for effective contribution of insectivorous birds' to arthropod regulation, on-farm trees need not cover large areas of the cropland as this may reduce acreage for the main crop. This implies that even in situations where available land is critically limiting, conserving trees to facilitate birds'

arthropod suppression role is still achievable on the basis of land-sharing rather than land-sparing and this helps to side-step concerns regarding diminished acreage and crop yields.

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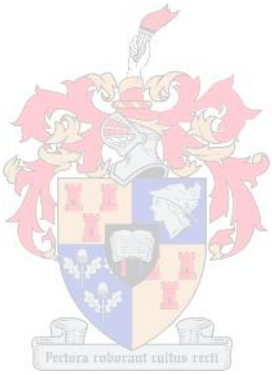

Chapter 5: Effectiveness of natural top-down regulation of herbivorous arthropod abundance at the landscape scale

5.1 Abstract

Habitat management for fostering increased populations of natural enemies of herbivorous arthropods towards biological control requires management strategies at both the local farm level and at the wider spatial scales. To determine the influence of spatial scale on arthropod and bird assemblage patterns across non-Bt maize farms, I grouped 16 farms into 5 clusters along gradient of structural heterogeneity and cover pattern, and compared assemblage responses between organic and conventional farming systems and also between mono-cropped and inter-cropped maize-fields. Structural attributes measured included hedgerow volumes, on-farm tree heights and densities as well as woodlot sizes. Cover characteristics included maize cover proportion, overall crop cover and crop diversity. In addition, I used analyses of $\delta^{15}N$ and $\delta^{13}C$ stable signatures in predacious and herbivorous arthropod tissues as well as their food sources, to evaluate predator roles in reducing herbivore abundance. I similarly compared assemblage turnovers of insectivorous birds and their herbivorous arthropod prey along the heterogeneity gradient to underpin birds' contributory role in reducing crop herbivory. Results showed that thick hedgerows were significant predictors of overall bird abundances while tree-dense regions attracted more species of insectivorous birds but those with larger woodlots enhanced overall bird diversity. Conversely, proportion of maize-field cover was the only major determinant of arthropod assemblage similarities across the landscape but in conjunction with hedgerow volume, while the role of predatory arthropods in regulating abundance of arthropod herbivores, though boosted by overall habitat complexity, was highest at moderate heterogeneity levels. However, there was no significant landscape-level role in insectivorous birds' contribution to arthropod herbivore regulation population reduction, even though both groups had significantly wide distribution across maize-dominated landscapes. Similarly, were no significant effects of crop diversity, farming system, cropping method or hedgerow type on arthropod or insectivorous bird compositional assemblages, though organic farming boosted abundance of birds overall. I conclude that although only a narrow range of ecological benefits of local-based low-impact field management techniques are realized at the landscape context, such practices remain important but need to be spatially up-scaled to area-wide programmes to achieve greater effect, particularly to enhance insectivorous birds' contribution to herbivorous arthropod reduction.

***Key words*:** Maize; Landscape context; Heterogeneity gradient; Up-scaling

5.2 Introduction

Agricultural land management systems greatly impact biodiversity (Sala et al., 2000; Flohre et al., 2011; Hawro et al., 2017) such that the consequences of land management regimes either benefit biodiversity such as through habitat extension (Whittingham et al., 2009; Zufiaurre et al., 2017) or adversely impact them such as through habitat degradation or loss (Donald et al., 2001). Conversely, wild species may impact crop production negatively through arthropod herbivory, or positively through provisioning of ecological services such as pollination, nutrient cycling or biological regulation of herbivorous arthropod populations (Landis et al., 2000; De Groot et al., 2002; Wolts et al., 2012). Land management methods that maximize the benefits derived from hosting biodiversity in croplands while minimizing crop losses to herbivorous arthropods are therefore likely to be most successful in promoting sustainable agriculture (Bianchi et al., 2006; Norton et al., 2009). This is particularly so for farmers who operate on small scale and are faced with the economic challenges of sustainably managing arthropod herbivore abundance by use of pesticides (IFPRI, 2004; Roubos et al., 2014; Horassa et al., 2016). Not only do agrochemicals lead to long-term soil degradation but they also minimize populations of beneficial predatory arthropods that may naturally prevent build-ups of herbivorous arthropod populations (Desneux et al., 2007; Aktar et al., 2009).

In that regard, increasing farm structural and land cover complexity through crop diversification, maintenance of semi-natural margins or planting on-farm trees are some of the field management techniques that have been shown to enhance benefits of wild species on croplands (Olufemi et al., 2001; Khan et al., 2006; Lemessa et al., 2015). In addition to hosting beneficial arthropods to reduce abundance of herbivores (Rusch et al., 2010; Rusch et al., 2016), more structurally complex configurations and land cover patterns also support higher abundances of arthropod pollinators while networks of farm trees and hedgerows also attract insectivorous birds that together contribute to more integrated suppression of arthropod herbivores (Tscharntke et al., 2008; Johnson et al., 2010). Organic farming system is considered as one way of improving such habitat heterogeneity towards natural herbivore regulation and is often applied together with various forms of crop diversification including inter-cropping, rotation or planting matrices of crop varieties to enhance cover diversification thus attracting diverse predatory arthropods (Norton et al., 2009). The system also entails minimal use of agro-chemicals such as pesticides, herbicides and inorganic fertilizers in management of pests or weeds, and is as such considered a viable strategy for offsetting farm input expenses for small-scale farmers, while also promoting environmentally sustainable agriculture (Dicks et al., 2013; FAO, 2014).

However, while the role of structural complexity in supporting predator-herbivore interactions is well documented (Beecher et al., 2002; Bengtsson, et al., 2005; Macfadyen et al., 2009; Letourneau et al., 2011; Lichtenbert et al., 2017), it remains largely unclear how such interactions and the herbivore regulation function is influenced by habitat structure and land management variables at the wider landscape level, especially for the case of maize-fields. To prescribe appropriate land use measures for increasing benefits of natural reduction in arthropod herbivory using habitat management, it is important to understand how predator-prey interactions respond to land management practices at both the local and wider spatial scales (Aviron et al., 2005; Veres et al., 2013). This is because arthropod predators and herbivore species have different habitat requirements, foraging ranging and dispersal patterns and are therefore impacted differently by habitat structure at various levels (Schmidt et al., 2005; Luck and Daily, 2003; Wolts et al., 2012). For instance, winged arthropods exploit habitats both within and beyond croplands; many birds use farmlands for foraging but roost further away; while various life stages of many winged arthropods such as lepidoptera interact with the agroecosystems in spatially and functionally differentiated patterns depending on life stages and forms (Klemola et al., 2010; Munoz-Saez et al., 2017)

Therefore, understanding multiple-scales effects of agricultural field management systems on predator roles of arthropod herbivore abundance regulation or differential turnovers in general, will help in land use planning across the agricultural landscape towards achieving more spatially-integrated practices for effective biocontrol of arthropod herbivores. Subsequently, using such information in agricultural extension efforts will trigger increased support from landowners to adopt appropriate methods for conservation of beneficial arthropods and birds across farming landscapes (Müller et al., 2010; Hovick et al., 2013).

My aim in this chapter was to evaluate how habitat measures and field management systems under organic or conventional farming systems, and monocultured or inter-cropped non-Bt maize, affect arthropod and bird compositional assemblages along a spatially explicit structural complexity gradient, and implications of such effects on natural regulation of herbivorous arthropods by predacious arthropods and insectivorous birds. I expected that increasing overall habitat structural and cover complexity at progressively higher spatial levels would be supportive of higher populations of predators and their interactions with herbivorous arthropod prey thereby enhancing overall landscape-level resilience against arthropod herbivory.

5.3 Materials and methods

5.3.1 Study area

I conducted the study in Kakamega Country, Kenya located 00º11'-00º26'N and 34º44'-34º51'E (Fig. 5.1), across a mainly subsistence agricultural landscape dominated my non-Bt maize fields, isolated native trees or stands of indigenous or non-native woodlots. Most farms were surround by live hedgerows and many farmers also kept a few heads of livestock (Garcia et al., 2009; Personal observation). Rainfall averages approximately 1,800 mm and temperature 21.4ºC annually, respectively (Kenya Meteorological Department, 2017).

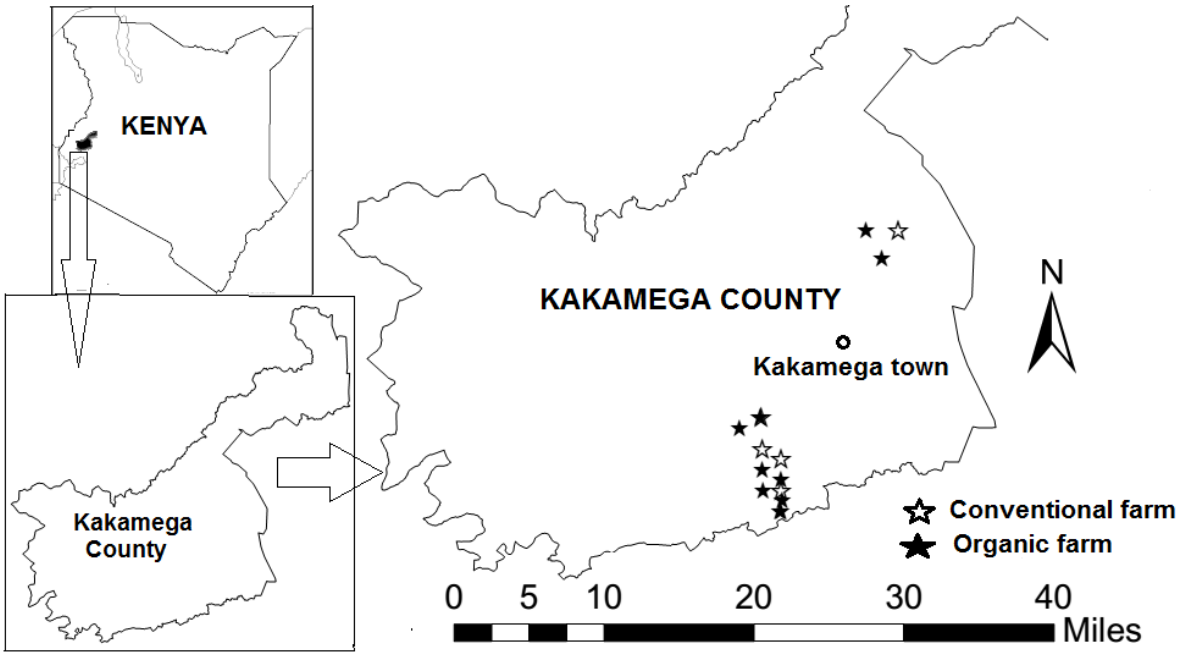

Fig. 5.1. Study area showing locations of study farms by farming system categories.

Organic farming was individual farmer-based with no official regulation. Many such farmers apply only organic manure to the soil, intercrop maize with other crops, rotate crops seasonally or plant different crops on multiple plots and fallow some parts of the farm occasionally. This contrasts with the case for farmers practicing conventional farming, who use inorganic chemical fertilizers at least twice during maize crop's growth, and seldom practice rotation, only occasionally diversity crops or leave uncultivated portions. Conventional farms are also slightly larger and are surrounded by either exotic hedges or just barbed wire. I undertook field work at three crop stages for each of two planting season (short rain season: October-January, and long rain season: March-July). The cropping stages were: early-crop (from germination to first weeding), mid-crop (from second weeding through flowering to cob formation) and mature-crop (from cob hardening to harvesting).

5.3.2 Selection of study farms

I selected a total of 16 farms of which 9 were organic and 7 conventional, within which were 9 where maize was mixed-cropped with legume crops and 7 were maize monocultures. Eventually, the farms selected comprised 3 mono-cropped organic, 6 inter-cropped organic, 4 mono-cropped conventional and 3 inter-cropped conventional fields.

For habitat farm variables, I measured maize-field cover as a percent of total farm size; woodlot size; hedgerow volume; tree height and tree density and also determined crop diversity as total number of crop-field types. I determined hedgerow measures with a tape measure and metre rule, to the nearest metre for length and to the nearest centimetre for height and lateral width. I measured hedge height and width at 20-m intervals. I also recorded counts of trees for each farm and used a clinometer to determine tree heights. Farms were also characterized by the nature of the dominant tree type and hedgerow if it was indigenous, exotic or no tree present (none). I ensured sampling independence by maintaining a minimum of about 500 m inter-farm distance (Beecher et al., 2002). Farming system and cropping methods, hedgerow type and tree type together constituted farm biotope factor variables while the other farm habitat measures were environmental variables.

5.3.3 Farm landscape clustering

In order to test the effects of farm biotope and habitat measures on bird and compositional assemblages at the landscape spatial scale and compare these with effects at the local farm level, I grouped farms into five cluster bands along a heterogeneity gradient integrating key structural (tree density, mean tree height, hedgerow volume) and cover pattern (crop diversity and percent maize cover) features (Gustafson and Parker, 1992; Flohre et al., 2011).. I derived these by summing up ranked values for each farm, based on a three-band score (1 = low, 2 = medium and 3 = high). Thus, heterogeneity index was calculated as: HI = (Dt+Ht+Vh+Dc+Cm) where HI = heterogeneity index for each farm and Dt; Ht, Vh, Dc and Cm are, respective rank band scores for tree density, mean tree height, hedgerow volume, crop diversity and percent maize cover. Maize cover percent was useful in surrogating total landscape crop cover size because during any cropping season in western Kenya, much of the landscape is dominated by maize fields (Laube et al., 2008). Similarly, crop cover proportion, together with crop diversity are often a close approximation of overall landscape cover diversity (Thies et al., 2003; Roschewitz et al., 2005: Hawro et al., 2017). I further assigned each of the derived farm clusters a heterogeneity score arising from averages of the respective component farms and this was included as further independent variable in all analytical models.

I surveyed birds using DISTANCE sampling protocol with line transects (Thomas et al., 2010). The survey entailed moving at a steady walking pace along a 60-m fixed-width transect centred along the farm's centre line (30 m each side), and I observed birds using a pair of binoculars and, on detection, identifying them to species. I also recorded bird cluster sizes and perpendicular distances in metres from transect centre, determined by a laser range finder (Bibby et al., 2000). While I observed the birds, a partner recorded the observations and these surveys were conducted in clear weather between 06:00 hrs and 11:00 hrs to capture the period of maximal activity and detectability (Bibby et al., 2000). Birds in flight were included only when detected from the front of the observer to reduce multiple counting of same individuals or groups (Bibby et al., 2000). For species moving in flocks, perpendicular distance was measured to the central point of the flock.

I collected arthropod samples using both sweep nets and un-baited pitfall traps which consisted of plastic cups of 70 mm diameter and 120 mm height, inserted into dug out holes with their rims flush with the ground (Gaigher et al., 2016), and filled to one-third with 25% sodium chloride solution for preservation as well as maintenance of chemical integrity for isotope analysis (Florencio, et al., 2011). I erected conical plastic rain guards above the traps for protection from direct rain and randomly placed four replicates, at equally spaced intervals along a diagonal line across the maize-field and collected the traps after three days. To supplement sweep-netting and pitfall trapping, arthropods were further sampled on maize using actual pick search-and-pick on leaves, stems, flowers and cobs of cops using forceps, on the all maize plants along every 10^{th} row of each field. I subsequently sorted and identified the arthropods to species or morpho species (Samways et al., 2010) but spiders were identified to order. For isotope analyses of arthropod basal food sources, I collected samples from maize (C_4 plant), legumes inter-cropped with maize (C_3 plants) and a selection of field-margin and hedgerow crops (C_3 plants). I also grouped the identified arthropods into two main guilds: herbivores or predators. Both plant and arthropod samples, having been labelled each for respective farms where they were collected from, were oven-dried to constant mass before sub-sampling and packaging into tinfoil capsules in preparation for isotope analysis.

5.3.4 Sample treatment for isotope analyses

For $\delta^{13}C$ and $\delta^{15}N$ isotopes analyses, I sent the sub-samples of the prepared plant and arthropods to the Isotope Laboratory of the iThemaba Environmental LABS in Johannesburg, South Africa. Analyses were accomplished on a Flash HT Plus elemental analyzer coupled to a Delta V Advantage isotope ratio mass spectrometer by a ConFloIV interface (ThermoFisher, Bremen, Germany) as described in Oelbermann and Scheu (2010). The $\delta^{13}C$ and $\delta^{15}N$ values were expressed

as fractions of international reference standards Vienna Pee Dee Belemnite and air, respectively (Post, 2002). The difference (δ) in isotopic ratio between the sample and standards was calculated as: $\delta^{n}X = [(R_{sample}/R_{standard} - 1)]*1000$ where $\delta^{13}X$ is the parts per thousand difference (‰) between the ^{n}X isotope in the sample and that in the standard; R_{sample} is the ratio of heavier to the lighter isotope of the element carbon or nitrogen, and, $R_{standard}$ = the ratio of the heavier to the lighter isotope in the standard (Post, 2002; Fry, 2006).

5.3.5 Data analyses – the landscape context

Comparison of the local and landscape context in arthropod and bird assemblages to habitat measures and farming systems, formed the basis of my analysis in this chapter. I transformed tree counts into densities, hedgerow measures to volumes and woodlot cover to sizes per hectare. Along with maize cover proportion and crop diversities, I pooled these variables to derive the five heterogeneity gradient constituting the 5 farm clusters. I also pooled arthropod and bird data in a similar way, using Shannon index and inverse of Simpson's dominance as arthropod and bird diversities respectively, and species richness as the cumulative number of species across the farms and all sampling periods (Magurran, 1988; Pinkus-Rendón et al., 2000). I subsequently, derived all farm biotope factor and habitat variable measures for the landscape spatial scale from average values of the constituent farms in the respective clusters. It is on these that further analyses were conducted (Flohre et al., 2011).

5.3.6 Bird analyses using Distance

I grouped birds as either insectivore or herbivore following the nomenclature of and the guild assignment system used by Kissling et al. (2012) and Fry and Keith (2004) modified to incorporate generalist species. Bird abundances were initially determined as densities using the DISTANCE v. 7.1 software (Thomas et al., 2010). I determined bird densities by fitting detection functions for each species but on the global scale (Newson et al., 2008) such that each farm was treated as a separate transect within the study area. Having spatially standardized detection probabilities, I grouped species into four categories based on relative commonness of encounter. For species encountered at least ten times across all observations (common), I fitted individual detection functions. The rest were clustered into three bands: those encountered 7-9 times were grouped as 'uncommon', between 4-6 times as 'rare' and 1-3 as 'very rare', and I fitted one common detection function for each of the three bands so that. Eventually I fitted total of 23 detection functions.

Global fit of detection functions for densities suited these analyses because the maize farms represented a standardized habitat type and thus no significant differences in bird detection probabilities were expected (Bibby et al., 2000; Thomas et al., 2010). For flocking species

encountered at least thrice during a survey, the cluster size used for the detection was the average of all cluster sizes observed for that species or group on that particular farm. This was to minimize cumulative errors associable with flock cluster size estimation (Meadows et al., 2012). I based the detection function model selections on the lowest Akaike Information Criterion (Thomas et al., 2010). Majority of the models selected were half-normal with cosine adjustments of order 2 or 3 (Thomas et al., 2010). Subsequently, from the global densities derived, I estimated populations of each species for each farm based on each farm size using the relationship: $P_{Sn} = D_{Sn} * S_F$ where P_{Sn} = population of species *n*; D_{Sn} = global density of species *n*; S_F = farm size (Bibby et al., 2000).

5.3.7 Isotope analyses

From the SIA results, I used Bayesian Mixing Model (BMM) method in the stable isotope analysis in the R siar v. 4 package Library (Erhardt and Bedhart, 2013; R Core Team, 2013), to establish a baseline iso-scape of basal food source signatures. Subsequently, I used a multi-source BMM model to establish trophic linkages of the various consumers to the basal iso-scape through their intermediary food sources or prey (Ogden et al., 2005; Girard and Baril, 2011), incorporating appropriate trophic enrichment factors (TEF). TEFs represent average (Mean±SD) incremental turnover values by which stable isotopic signatures change from food source to consumer tissues up the food chain during the process of metabolic fractionation, (Phillips and Gregg, 2003; Fry, 2006). The BMM functions on the basis that constructing a $\delta^{15}N$ / $\delta^{13}C$ food sources bi-plot creates a food source iso-space polygon that delineates $\delta^{15}N$ and $\delta^{13}C$ qualitatively and quantitatively for each consumer (Bond and Jones, 2009). The TEFs that I applied for herbivorous arthropod consumers were averages according to reviews by Spence and Rosenheim (2005) and for predacious arthropod consumers, averages arising from review for terrestrial invertebrates by Caut et al. (2009) and Ferger et al. (2013). Subsequently, I evaluated relative contribution of maize (RCM) and the other plant food sources to the diets of consumers (herbivorous and predacious arthropod groups) (Ogden et al., 2005; Erhadt and Bedrick, 2013). This enabled determination of the extent to which arthropod consumer diets might be traced back to maize as a food source (Phillips and Gregg, 2003; Phillips et al., 2005).

5.3.8 Bird and arthropod response to habitat variables

I used Generalized Linear Mixed Models within the *nlme* package in R version 3.4.2 (R Core Team, 2017) to assess landscape-scale relationships of farm biotopes and habitat variables to bird and arthropod assemblages, and evaluate the regulation potential of predacious arthropods on herbivores (Bolker et al., 2009). I fitted the models with Poisson error probability distribution and log-likelihood link function for species richness and abundances, binomial error distribution with

logit link function for diversity indices and relative contribution of maize (RCM) to arthropod consumer diets (Bolker et al., 2009). I included farm number as a random variable in the models with farm biotopes and environment habitat measures as fixed factors. For bird dependent variables, I again included arthropod abundance as additional predictor variables.

I used Distance based Linear Modelling (DistLM) in PRIMER version 6.1 software (Primer-E, 2008) in identifying farm habitat attributes that best explained arthropod and bird compositional assemblages along the landscape scale complexity gradient. Again for the case of insectivorous birds and predatory arthropods' roles in arthropod herbivore reduction, I included species richness and diversities (Shannon or Simpson's index) as additional independent variables. I ran DistLM models on square-root transformed Bray-Curtis similarity matrices of abundance data for birds and arthropods, and on normalized similarity matrices on Euclidean distances for environmental data (McArdle and Anderson 2001). I ran models stepwise and selected suitable models based on Akaike Information Criterion adjusted for small sample size (AICc) to reflect the reduction of number of farms from 16 to the 5 as a results of clustering.

5.3.9 Insectivorous birds' predation role on herbivorous arthropods

To assess influence of habitat factors on the insectivorous birds' predation on herbivorous arthropods, I conducted analysis of covariance (ANCOVA) to test the combined influence of farming system on bird and herbivorous arthropod aggregations with the goal of assessing the scenario of maximal impact of birds on herbivorous arthropods. To meet assumptions of ANCOVA, the two bird-herbivorous arthropod dependent variables selected had to be moderately correlated, normally distributed and with variance homogeneity, confirmed using Box's M test (Nakagawa and Cuthill, 2007). The correlation also needed to be negative in order to fit an inverse effect of birds on the herbivorous arthropod abundance. Based on these conditions, I selected bird species richness and herbivorous arthropod diversity as the dependent variables and farming system as independent variables while farm size was the fixing covariate as there was a high variation in farm sizes (mean = 3.20±0.66; std dev = 2.71). I assessed the overall multivariate effect of the independent variable in the ANCOVA test using Wilks Lambda value with Bonferroni correction to the confidence intervals of adjusted means. Finally, I conducted separate analysis of variance tests to assess univariate effects of the independent and covariate variables on the dependent variables

5.4 Results

I recorded 212 arthropod species or morpho species from 15 orders comprised of 51 families across the farms studied. For birds, 111 species representing 35 families were encountered, 80 insect-eating

species from 30 families and 34 plant eating species from 16 families, but excluding birds of prey or scavenging species.

PERMANOVA test results showed no significant spatial-scale differences in influences of farm habitat measures or farm biotopes (farming system, cropping method or hedgerow type) on assemblage similarities of arthropods. However, from GLMM tests, (Table 5.1) overall bird abundance and diversity were enhanced under organic farming systems (Table 5.1; Fig 5.2). Insectivorous birds were more species rich across landscapes characterized by larger woodlot stands and higher herbivorous arthropod abundances (Table 5.1) while overall bird diversity was boosted by higher tree densities across the landscape (Fig 5.2). Insectivores were also more species rich in spatial regions that were richer in herbivorous arthropod species.

Table 5.1. Generalized Linear Mixed Model (GLMM) test results showing significant effects of habitat measures and farm biotope effects on bird compositions at the landscape spatial scale. Bird diversity represents the Shannon diversity index. Significance was pegged at $p<0.05$.

Dependent variable	Predictor	Dependent variable measure		
		Abundance	Species richness	Diversity
Birds overall	Tree density (per ha)	-	-	0.033
	Farming system	0.050	-	0.042
	Hedgerow volume (m^3)	0.016		-
Insectivorous birds	Woodlot size (ha)	-	0.054	-
	Herbivorous arthropod species	-	0.010	-

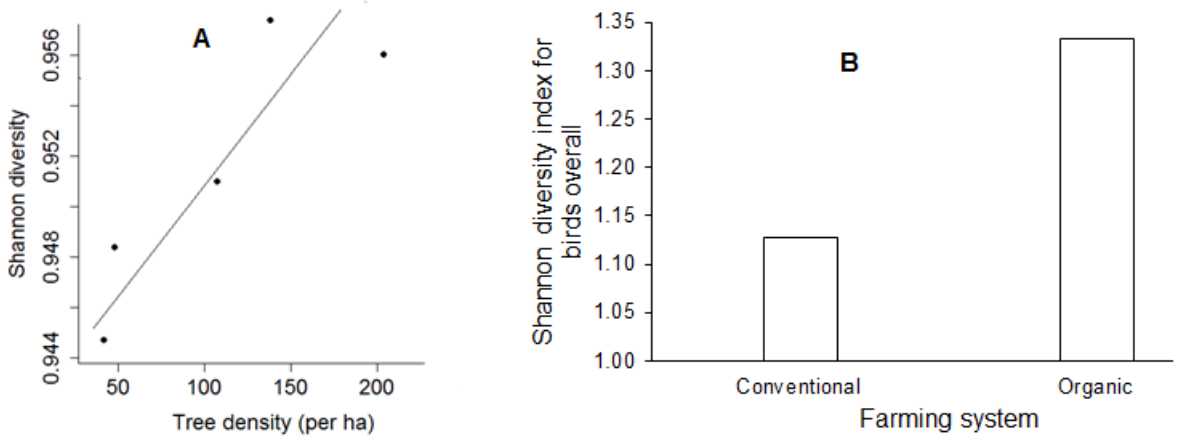

Fig 5.2. Influence of A) tree density and B) farming system on diversity of birds overall.

Although no effect of farm biotope factors was observed on assemblage similarities of any arthropod feeding guild, from the PERMANOVA tests, DistLM tests showed maize cover percent as predominantly influential in assemblage similarities of all three arthropod guilds at both local and wider spatial levels (Table 5.2).

Table 5.2. Distance-based Linear Models (DistLM) tests, based on Bray-Curtis similarity index, showing habitat variables that contributed most to landscape-scale variations in similarities of arthropod and bird assemblage patterns. Significant effects ($p<0.05$) are in bold face.

Dependent variable	Predictor variable	Pseudo-F	p	Proportion contribution	Cumulative contribution	Percent explained	R^2
Predacious arthropods	Maize cover (%)	1.574	**0.041**	0.344	0.344	54.3	0.868
	Crop diversity	1.510	0.364	0.199	0.543		
Herbivorous arthropods	Maize cover (%)	2.135	**0.008**	0.416	0.416	83.5	0.876
	Crop diversity	0.840	0.567	0.219	0.635		
	Hedgerow volume	0.748	0.690	0.200	0.835		
Arthropods overall	Maize cover (%)	1.747	**0.033**	0.368	0.368	81.8	0.850
	Crop diversity	1.059	0.414	0.261	0.629		
	Hedgerow volume	0.703	0.826	0.190	0.819		

Similarly, despite no significant spatial-scale variation in effect of farm biotopes, hedgerow volume significantly impacted variation in bird assemblage similarity ($F = 2.460$; $p = 0.049$, AIC = 36.9), explaining 45.1% of the variation. There were no influences of farm biotopes or habitat variables on assemblage similarities of either insectivorous birds or birds overall.

One-way ANOVA showed a significant difference in proportion of maize carbon (RCM) for consumers' overall across the three structural heterogeneity levels ($F = 6.459$, $p = 0.021$), with subsequent within-group Tukey LSD test indicating that the main significant source of this variation was between the 'low' and 'medium' structural heterogeneity levels ($t = 0.840$; $p = 0.044$). Overall proportion of dietic carbon in consumer diets peaked at moderate landscape heterogeneity levels but reduced more dramatically for herbivorous arthropods at the highest habitat complexity (Fig 5.3). There was no differences in RCM between the guilds themselves ($F = 3.209$; $p=0.587$, df = 2).

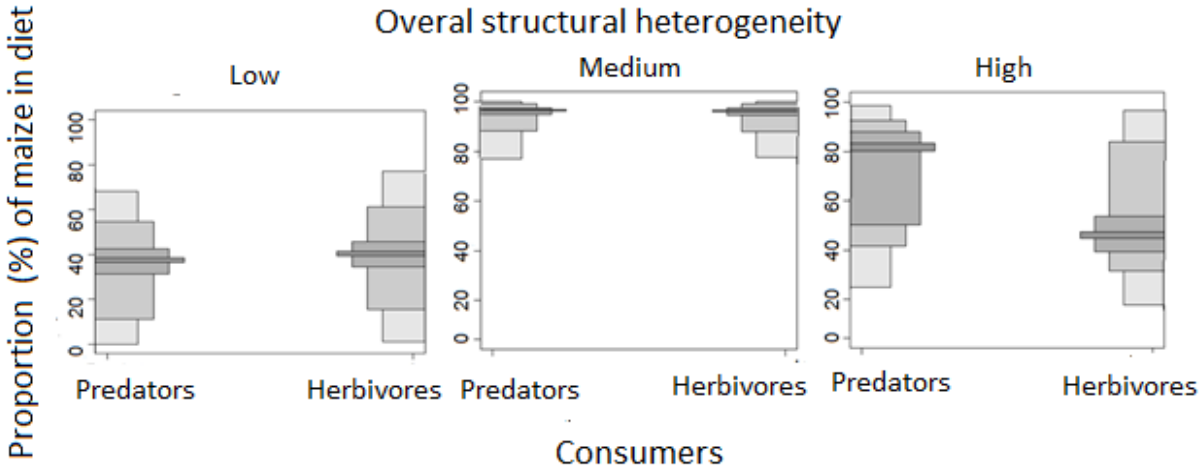

Fig 5.3. Comparative variations in proportion of maize carbon (RCM) to diets of predators and herbivorous arthropod groups across the three levels of farm structural heterogeneity clusters.

The type of tree dominating the landscape had a strong effect on the level of maize carbon in predacious arthropod diet (χ^2=7.071; p=0.0194) with indigenous tree dominance being consistent with higher relative contribution of maize (RCM) to predacious arthropod diets (Fig. 4). However, there was no significant intra-spatial scale variation in predacious arthropod RCM response to farming system, cropping method or hedgerow type. In the same way, no habitat measure of farm biotope factor had any influence on herbivorous arthropod RCM across the spatial gradient.

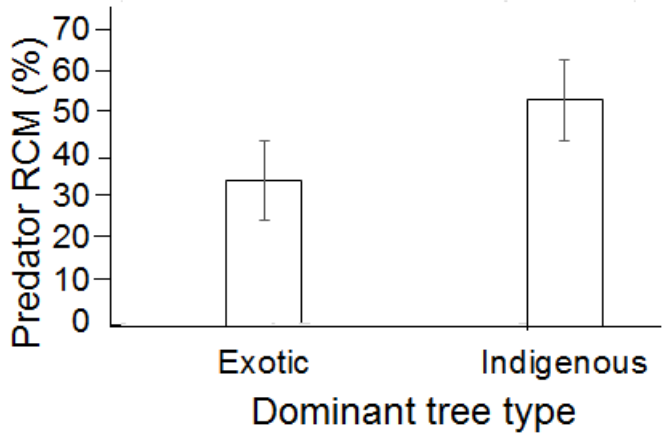

Fig 5.4. Influence of type of dominant tree type on relative contribution of maize (RCM) to diet of predacious arthropods at the landscape spatial scale. Error bars represent standard errors.

Insectivorous bird abundance was influenced by hedgerow volume at the wider landscape scale but not at local-farm scale $\chi^2 = 4.888$; $p = 0.016$. Insectivorous bird species richness, on the other hand significantly increased with richness of herbivorous arthropod species ($\chi^2 = 6.022$; $p = 0.009$) but showed only a weak response to average woodlot size ($\chi^2 = 3.078$; $p = 0.0542$) see Fig 5.5, and to heterogeneity index as a variable ($\chi^2 = 3.124$; $p = 0.058$).

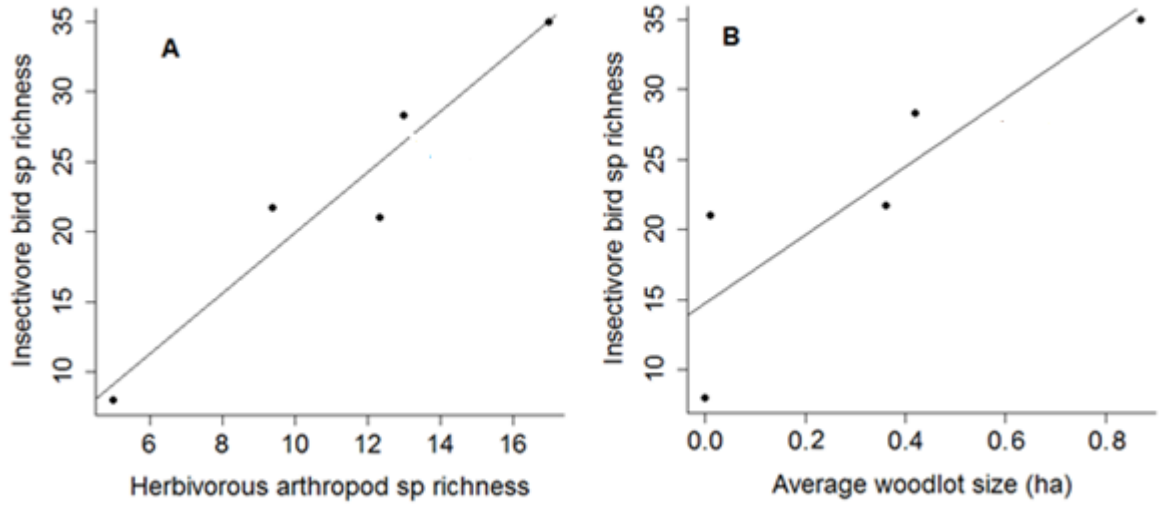

Fig 5.5. Regression plot of effect of A) herbivorous arthropod richness and B) average woodlot cover size on insectivorous bird species richness at the landscape scale.

There were no effects of any habitat variable on insectivorous species diversity. Similarly, there were no effects of farm biotopes on abundance, richness or diversity of insectivorous birds. Herbivorous arthropod abundance, species richness and diversity were also not influenced by any habitat variable or farm biotope at the beyond-farms scale. Conversely, DistLM results showed that assemblage similarity of herbivorous arthropods were significantly influenced by maize cover at the landscape scale ($F = 2.135$, $p = 0.008$). The best combination of habitat variables to influence herbivore assemblages was maize cover together with crop diversity ($F = 0.840$, $p = 0.567$) and hedge volume ($F = 0.748$, $p = 0.690$), together explaining 83.4% of the assemblage similarity variation though the latter two were not themselves individually significant. Farming system, cropping method or hedge type did not influence herbivorous arthropod assemblage at this beyond-farm level.

From the ANCOVA test of bird-herbivorous arthropod predatory linkage, the multivariate overall test returned a non-significant effect of farming system on the combined response of insectivorous bird species richness and herbivorous arthropod diversity at the landscape scale

(Wilks lambda score = 0.394, F = 1.540, p = 0.432, df = 4). For univariate within-groups ANOVAs, farming system did not significantly influence insectivorous bird species richness (F = 1.540, p = 0.432) nor herbivorous arthropod diversity (F = 0.051, p = 0.859).

5.5 Discussion

Effects of the range of farm qualitative attributes on arthropod and bird compositional assemblages and interactions at the landscape scale were generally quite low as compared to the local effects outlined in chapter 2 and chapter 4, respectively. Farm biotope factors such as farming systems and cropping methods were particularly ineffective in driving assemblage responses or trophic linkages between invertebrate and bird predators and their potential prey beyond local-farm spatial levels. This reflects the generally localized and farm-based nature of organic system adoption by farmers in the study area, a factor which resulted to equally localised ecological benefits this system (Tscharntke et al., 2007; Moyo, 2010; Wolts et al., 2012). Similar findings were reported by Lichtenberg et al. (2017) who, in a global synthesis, found that arthropod diversity increased primarily at the local farm levels under organic farming regimes, even though richness and abundance were enhanced at multiple spatial scales. Multiple spatial scale enhancement of abundance were also observed for organic farming by Inclan et al. (2015) for some species of tachinid parasitoids (Tachinidae, Diptera).

Despite the insignificant role of farm biotopes on overall arthropod assemblage patterns beyond the farms, organic farming seemed to provide a conducive environment for more diverse birds in general as compared to arthropods. This indicates that birds generally use the resources at a larger spatial scale than arthropods, particularly due to their relatively larger sizes and wider foraging ranges (Kellermann et al., 2008; Lemessa et al., 2015). Beecher et al. (2002) showed similar responses of bird feeding guilds in surveys across paired organic and conventional fields in Nebraska, although the study was conducted on a single large farm estate.

Hedgerows and trees also constituted significant landscape structural attributes in driving bird assemblage responses. As such, despite hedgerow type appearing to be seemingly unimportant in determining bird assemblage patterns, thicker hedgerows attracted larger aggregations of birds and this shows that even at the landscape scale, hedges are important substrate components of the agricultural habitat for bird communities and may be used as dispersal corridors, foraging or even nesting habitats (Hinsley and Bellamy, 2000; Munoz-Saez et al., 2017). Landscapes characterized by dense on-farm trees and woodlots were equally attractive to diverse bird communities particularly insectivore species. Many insectivores use trees as foraging substrates, territorial or home range staging posts (Whittingham, et al., 2009; Newmark and Stanley, 2016) while woodlots are important as extensions of natural nesting and roosting habitats (Personal observations).

Insectivores were also more species rich across farm landscape clusters that were correspondingly richer in herbivorous arthropod species, suggesting a close trophic linkage to potential herbivorous arthropods and thus underscoring the birds' contributory role in landscape level provisioning the ecosystem function of top-down arthropod herbivore regulation (Bianchi et al., 2006; Johnson et al., 2010).

For arthropods, maize cover proportion across the landscape was the only important determinant of assemblage patterns in herbivores, which shows the importance of maize as a basal food source for most arthropods, but this finding may also be simply due to the predominance of maize-fields as a landscape feature in the study region. The influence of maize cover for arthropods overall, was particularly prominent in combination with thicker hedgerows and diverse crop-field types, and this suggests that although maize may be important to herbivorous arthropods as a food source and to predacious arthropod as a foraging ground for prey, adjacent crop-fields and hedgerows may themselves serve the purpose of refuges and alternative food sources alongside or in the absence of maize (Geiger et al., 2009; Rush et al., 2010; Munoz-Saez et al., 2017).

The influence of landscape-scale habitat complexity on removal rate of herbivorous arthropods by predacious arthropods, represented here by proportion of maize in consumer diets, with almost equal maize carbon proportions in both predators and herbivorous arthropods at the lowest landscape-complexity level indicates a balancing of structural effects at the local level where both trophic groups derive less than half of their total organic carbon from maize due to variety of local-level crop food source options (Dassou and Tixier, 2016). At moderately higher landscape complexity levels, there is a sharp rise in maize consumption up to a peak when both guilds obtain nearly all of their carbon from maize, perhaps due to increasing dominance of the maize food relative to other source across the landscape. Finally, at the highest landscape complexity, there occurs a sharp drop in maize dependency for herbivorous arthropods but nearly no change for predators. This suggests a reduced dependence by herbivorous arthropods on maize food sources at the highest landscape structural heterogeneity at which there are presumably more plant food source options (Tews et al., 2004; Hovick et al., 2013) while for predators, particularly those with specialized diets, there is still dependence to a large extent on equally specialist maize consumers as prey items. This indicates the significance of increasing landscape complexity as management measure for potentially increasing effectiveness of predatory in regulating maize-consuming herbivores such that more structurally heterogeneous landscapes can support sufficiently higher predation rates even in cases where maize dominate such landscapes. (Thies et al., 2003; Fabian et al., 2013),

Surprisingly, levels of trophic maize carbon in predacious arthropod diets were further enhanced by landscapes dominated by indigenous trees, implying that some of these predators may

utilize such trees for breeding purposes or that decomposing leaf litter from such trees may provide suitable micro-habitat to support predators' early developmental stages (Culliney, 2013; Paudel et al., 2015). It may also arise from most farmers' tendency to plant such indigenous trees either at the field margins, or as woodlot stands at farm corners, both spatial segments constituting habitat boundaries where spiders, in particular, occur at higher abundances as was noted by Clough et al. (2005). However, there was no connection of any farm biotope attribute to maize carbon levels in predator or herbivore arthropod diet at the higher spatial scales, again showing the limited influence of farming or cropping systems on arthropod linkage to maize diet beyond the local farm scale.

Although there were positive multi-scale responses of insectivorous bird assemblages to hedgerow volume and arthropod herbivore diversity, thereby underpinning the bird-to-herbivore trophic connection (Benton et al., 2002), neither these habitat measures nor any of the farm biotopes influenced the combined covariation of insectivorous birds and herbivorous arthropods. This further points to the spatially differentiated perspectives of farm structural attributes between birds and arthropods in terms of their dispersal ranges, with the latter being more localized while former range more widely (Kellerman et al., 2008; Lemessa et al., 2015). Therefore while the trophic connection between these taxa was functionally evident at the local scale through the exclusion experiment, this connection may be distorted by landscape-level structural configuration patterns. Wenny et al. (2011) noted that because birds are highly mobile and range widely across the agricultural landscapes, improving their roles as agents of herbivorous arthropod suppressers should focus more on wide spatial-level habitat structural manipulations for effective results.

Farming system and cropping methods were equally unimportant in influencing combined assemblages of insectivorous birds and arthropod herbivores even though variations in the distribution pattern of arthropods showed a strong separate dependence on maize cover proportion across farms. In a similar response mismatch, hedgerow volume and tree characteristics that were both important in determining insectivorous bird assemblage and composition elicited no corresponding response from herbivorous arthropods. This suggests that at the wider spatial levels, only habitat variables that affect both insectivorous birds and herbivorous arthropods in terms of both distributi7on and composition, are likely to sufficiently strengthen the trophic connection between the two taxa to effectively maximize the bird' contribution to herbivorous arthropod herbivore. This finding means that while managing farms to boost general habitat complexity and cover diversification may be enough to build up populations of predatory arthropods at the local farm scale, more complex habitat management mechanisms are required at wider spatial scales to achieve the same beneficial impacts by vertebrate predators such as insectivorous birds (Chaplin-Kramer et al., 2011).

5.5.1 Conclusion

The results of this chapter demonstrate that beyond the local farm level, structural aspects of agricultural habitat are generally more consequential than field management systems such as farming or cropping regimes, in shaping composition, distribution and interactions of arthropod and bird communities. This is in contrast to findings in chapter 2 and chapter 4 where these habitat variables had more significant influences on arthropod and bird assemblage responses. Furthermore, although organic systems of farming are in general associated with more complex farm habitat structures, the usually more localized focus of their application by farmers undermines their potential role in enhancing wider interactive and functional connectivity amongst species, particularly with regard to improving the role of predators in top-down reduction of herbivorous arthropod populations. This presents an opportunity for upscaling of such habitat management methods so as to expand the benefits of their influence on predator-prey trophic linkages for effective biocontrol. Therefore, encouraging farmers to adopt appropriate habitat management systems at wider regional levels can boost the spatial scope of ecological benefits across functionally interconnected farms and ultimately contribute to higher resilience of the farming landscapes against crop damage by herbivorous arthropods (Folke et al., 2004; Lin, 2011). Chaplin-Kramer et al. (2011), demonstrated that creating a conducive habitat at multiple spatial scales is particularly important for generalist arthropod predators because they exhibit distinct assemblage responses and connection to their prey at both local as well as wider spatial levels.

5.6 References

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Chapter 6: General discussion and synthesis of overall findings

6.1 The role of farming systems and cropping methods

The importance of choice of farming-system in naturally managing herbivorous arthropod abundance across the maize-fields runs prominently across all chapters in this study. The overriding importance of organic farming system in minimizing environmental impact due to non-use of chemicals (Tuomisto et al., 2012) and improving structural heterogeneity to boost predacious arthropod abundance, is clear in chapters 2 and 3. This clearly contrasts to conventional systems typified by simplified habitat and landscapes favouring primary consumer taxa while discouraging predators thereby increasing crop-field susceptibility to proliferous herbivory (Letourneau and Goldstein, 2009; Bianchi et al., 2006). However, the potential of low-intensity agricultural systems such as organic farming to meet the global demand for increased production for higher human population, is often criticized on the basis of lower crop yield levels in comparison to the more intensive conventional systems (Connor, 2008; de Ponti et al., 2012). Such criticisms are however, seldom backed by detailed comparison of the full range of capital, habitat or environmental costs of production, to the respective net returns (de Ponti et al., 2012; Sudheer, 2013). Quite often, the net returns significantly justify low-impact farming as the more financially and environmentally sustainable form of agriculture (Gomiero et al., 2011; de Ponti et al., 2012; Eden et al., 2017).

In contrast to farming system, the importance of cropping method was not necessarily uniform at all levels. For example, it is worth noting, that in chapter 2, 4 and 5, the role of cropping methods was diminished in comparison to farming system. In chapter 2, inter-cropping had no effect on herbivorous arthropods, and also affected only (positively) predacious arthropod diversity, not abundance or richness. By comparison, organic farming enhanced abundance and diversity of predacious arthropods while conventional farming boosted abundance of herbivores. Similarly, in chapter 4, there was no influence of cropping methods on insectivorous birds or on their potential herbivorous arthropod prey, but the herbivorous arthropods were more abundant on conventional farms. In chapter 5, again inter-cropping affected neither arthropod or insectivorous bird assemblage response to habitat variables, nor the potential role of the birds' contribution to herbivore regulation along the spatial scale gradient despite organic farming corresponding to overall bird abundance at all levels. However, in chapter 3 that entailed isotope analyses, the trophic linkage between predators and herbivorous arthropods was stronger under inter-cropped than mono-cropped systems, this being the main highlight of the role of cropping methods.

These findings imply that from the functional perspective of predators especially insectivorous birds, inter-cropping is basically a plot-level phenomenon. Therefore, although the

natural trophic link between predators and herbivore prey is potentially enhanced by inter-cropping to boost niche breadth due to higher habitat structural complexity, it would take beyond-farm application of systems such as organic farming to sufficiently reduce habitat simplification so as to substantially support natural enemies' overall role in herbivore suppression (Rusch et al., 2016). Thus incorporating inter-cropping within organic farming systems in maize-fields is important in improving plot-level as well as wider-scale effectiveness of predatory arthropods in their overall biocontrol role (Olufemi et al., 2001; Letouneau et al., 2009). In the case of chapter 3, the findings further highlight the significant role of stable isotope analyses technique in revealing the more subtle details of trophic interactions that are not readily detectable through classical field ecological observation methods. Thus it is only through isotope analyses that the role of cropping method was revealed. In the case of maize, this biocontrol role on herbivorous arthropods may be improved by inter-cropping maize with crops that have at least the same life-span as maize itself, in addition to the variety of pulse crop species that are more often inter-cropped with but which tend to mature earlier than maize. Similarly, insectivorous birds' contribution to herbivorous arthropod depredation is more enhanced if organic farming incorporates larger-scale structural habitat management and is practiced at both the regional as well as local scales. According to Silechi et al. (2008) inter-cropping maize with legumes has an additional benefit of boosting soil fertility and enhancing yields, thereby offering a suitable alternative to synthetic soil fertilization.

6.2 Roles of cover characteristics and landscape structural complexity

Crop diversification showed a superior role to inter-cropping in attracting both arthropods overall and insectivorous birds across the farms as illustrated in Chapter 4. This shows that a diversified cover structure even within the local farm level is an important incentive for abundant predacious arthropods, which can therefore range and forage more widely on the agricultural habitat (Railsback and Johnson, 2014). This positive role of cropland plant diversification on predator abundance was also reported from a review by Letourneau et al. (2011). For insectivorous birds in particular, a diversified matrix of crops and non-crop plants across the farm presents a horizontal heterogeneity that may offer a wider range of arthropod prey than can individual inter-cropped plots (Freemark and Kirk, 2001; Flohre et al., 2011). However, maize cover proportion as an element of horizontal heterogeneity appeared to be more attractive to herbivorous than to predacious arthropods because firstly, when maize dominates the landscapes it is more accessible as herbivore food source and, secondly, since it is grown nearly all year round, with only minimal temporal variations in availability, many specialist maize consumers have little need for temporal dispersal in search of alternative food.

Hedgerows represented the most important aspect of structural heterogeneity across all farms and appeared as the most profound incentive for assemblage composition of all arthropod and bird guilds as discussed in Chapters 2 through to Chapter 5. Hedgerow volume was a particularly strong driver of overall natural arthropod regulation through fostering aggregations and variety of arthropod predators and insectivorous birds. Hedgerows not only represent expanded habitats across the agricultural landscapes to support species as perching, nesting, forage and refuge resources but also serve as anti-predator vigilance posts and dispersal corridors for many taxa (Burel, 1996). Additionally, as elements of structural complexity, they help to diversify the habitat and increase niches for more species of beneficial arthropods (Morandin et al., 2014). Thicker hedgerows more efficiently supported higher aggregations of arthropod predators while elongated ones harboured multiple predator taxa at higher diversities thereby reducing clumping and species dominance. This factor is important in expanding spatial coverage of predatory roles to target more diverse prey. In natural indigenous form, hedges are also efficient in facilitating medium-term herbivore biocontrol because they then constitute semi-permanent habitat substrates across cropping seasons for the specialist predators such as wasps as well as the less mobile edge generalists such as spiders (Clough et al., 2005; Gareau et al., 2013). Therefore due to its positive influence on both arthropod and bird predators, hedgerows or strips of non-crop vegetation represent one of the most important structural features in integrated biocontrol of herbivorous arthropods across small scale maize-fields

On-farm trees, on the other hand enhanced habitat structural complexity in the vertical plain, offering a vertically stratified niche differentiation (Hovick et al., 2013; Munoz-Saez., 2017). They were particularly important in boosting insectivorous bird richness and diversity especially when present in dense tall stands, which facilitates birds' efforts to forage for invertebrate food, serving as scanning posts and as launching susrfaces for prey capture bouts. Tall trees are also important for roosting and dispersal across the landscape and as singing posts, mating contact stations or for territory defence. Since they have higher longevity and persistence across the farms as compares to hedges, trees also support bird predation on arthropods in the medium term, with woodlots which are perceived by birds as mini forests, particularly important as roosting and nesting habitat (van Bael et al., 2008).

6.3 Herbivorous arthropod suppression by predacious arthropods and insectivorous birds

Arthropod predators were generally more efficient than insectivorous birds in contributing to regulation of herbivorous arthropod abundance and this may be due to the closer contact between predacious arthropods to the substrate that hosts the herbivores, as compared to birds, which not only range widely but are additionally hampered by anthropogenic disturbance (Asefa et al., 2017).

In addition, unlike most arthropods, there is a spatial as well as temporal differentiation between foraging and roosting for birds further limiting the overall contact rate with arthropod prey. For instance, for many birds, nesting or roosting areas are located away from the farms themselves so that contrary to the case of predacious arthropods, birds-arthropod interactions are restricted to diurnal periods only, leading to comparatively lower efficiency of birds to impact arthropod herbivore abundance. This may however possibly be offset by the fact that birds can consume arthropods at higher rates than can predacious arthropods.

Amongst arthropod predators themselves, ants were evidently the best potential overall regulators of maize-field arthropod herbivory, particularly owing to their wide range of herbivore prey, and also for incorporating higher total carbon from both maize and legumes, compared to the other predators. This highlights ants' significant role in multiple-crop protection from herbivory. This role is further enhanced by ants' known communal foraging behaviour, high densities and exploitation of habitat in multiple spatial and temporal strata (Landis et al., 2000). Furthermore, ants' wide dispersal and distribution enable them to potentially reduce herbivorous arthropod populations over wide areas in a shorter period of time thereby minimizing potential for herbivore proliferation and spread, as compared to other predators that have more localized dispersal. However, the symbiotic association of ants to some hemipteran herbivorous species (Cranshaw and Redak, 2013), may increase vulnerability of certain crops to damage by such herbivores. It is encouraging, however that all arthropod predators showed significant isotopic carbon signatures of lepidopteran consumers in their diets, which indicates that lepidopterans are efficiently targeted for predatory regulation. This is because the lepidopteran group constituted the most prominent herbivores of both maize and legume crops. Overall, the best strategy for an effective natural reduction in maize herbivory should target conservation of earwigs; reducing legume herbivory should target conservation of wasps and predacious beetles, while a comprehensive field-wide herbivore biocontrol of consumers of booth maize, legumes and other plants should aim at conserving both ants and spiders concurrently. .

In the case of insectivorous birds' predation role, the exclusion experiment proved a clear bird-to-herbivorous arthropod trophic linkage to confirm the herbivorous arthropod abundance reduction function of birds' arthropod reduction contribution. This role of birds can evidently be augmented through low-impact farming, even though infrastructural developments and anthropogenic disturbance may somewhat limit realization of the full results. Effective habitat structural configuration management, is however, also essential in complementing the role of low-impact farming for successful natural biocontrol of arthropod herbivores (Freemark and Kirk, 2001).

Although performance of various systems of habitat management to control crop herbivory in Africa is still hard to evaluate due to lack of standardized systems of measure, appreciable success is already demonstrable in the case of maize. For example, effectiveness of the push-and-pull technique in managing *Busseola fusca* pest in maize and other cereals, which was first applied in Kenya ten years ago, has already been tried in other tropical regions (Cook, 2007' Poveda and Kessler, 2017). The method has also been extended to other such non-cereal crops as sugar cane in parts of South Africa where it is used in managing the cane borer *Eldana saccharina* Walker (Lepidoptera, Pyralidae) with a variety of grasses as companion crops in place of Napier grass (Conlong and Rutherford., 2009; SANBI, 2015). However, use of the companion crops approach to pest management has at times been cited as having negative impacts on sustainable yields of the main crops because the techniques require setting aside of some considerable acreage for the companion crops which often require as much care of as the main crop itself. Similarly uptake rates of such methods have remained lower than initial projections because they are widely perceived as rather too highly technical to the average farmer. In the case of rice, the concept of integrated biodiversity management to complement integrated pest management (IBM), was first proposed in 2000 (Kiritani, 2000) but has not registered as much success as was expected in Asia due to, firstly, unsustainability of government technical and capital support and, secondly, increased aggressive marketing by agrochemical corporation, for pesticides and transgenic rice varieties. In Africa, IBM is still at its infancy, but is mainly under the stewardship of non-profit agencies focussing on promoting farmer-based habitat management and farming diversification for increased net returns (Thorburn, 2015). Because of similar efforts by agrochemical corporations in Africa, there is as yet no chemical-free pest management scheme that is wholly farmer-driven.

Form the foregoing, it is evident that the success of habitat management practices to promote natural suppression of arthropod herbivore damage to maize would require farmer sensitization to clearly demonstrate the methodologies and highlight their inherent benefits. This would increase the rate of uptake as well as promote sustainability, as opposed to reliance on governments or NGOs for technical and financial support in the long term.

6.4 Landscape-level habitat management action to drive arthropod herbivore regulation

A desirable aim of natural crop pest reduction through low-impact agronomic field management is to promote landscape resilience against arthropod herbivory at both local and regional scales (Gabriel et al., 2010). This is however seldom realised when farmers adopt low-impact agronomy as individuals rather than collectively. As a result, and as revealed in this project, despite strong influences of organic farming systems, inter-cropping and crop diversification in fostering

arthropod herbivore depredation at the individual farm scale, beneficial impacts of such measures are bound to have minimal results at the beyond-farm spatial scale. Thick hedgerows and on-farm trees, including woodlots, were the only structural variables whose positive impacts on bird assemblages were replicated at local and regional scales, and the features potentially facilitate insectivorous bird's contributory role in mitigating arthropod herbivory.

The regional-scale influence of trees and hedgerows on bird assemblages but not on arthropod turnovers further emphasizes the former's wider perception of the agricultural landscape(Silva-Andrade et al., 2016), and their need for wider dispersal as a possible incentive to their contribution to arthropod herbivore reduction. Linkage of trees and hedges to bird assemblage did not however translate to significant roles of insectivorous birds in reducing abundance of maize arthropod consumers beyond the farm scale. This may suggest that at the wider spatial level, birds probably have access to a wider array of arthropod prey food sources that I was able to sample within the localized individual farms, at which level predominantly maize-associated arthropods may thrive. On the other hand, from the $\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses of consumer diets, the role of predacious arthropods in reducing arthropod herbivores was clearly evident at both local and wider scales, albeit at different magnitudes. This further underscores the importance of using stable isotope analyses as a tool in understanding finer-scale trophic associations across the agricultural ecosystem.

To sum up, effective management of herbivorous arthropod populations in maize-fields may be best achieved by managing farm habitat in such a way as to synergize the complimentary roles of the array of structural configuration variables with those of farming and cropping systems. This is because no single habitat measure showed any influence on the whole range of assemblage patterns that reflects a boost in predator numbers and a corresponding reduction in herbivorous arthropod abundance. Secondly, such management measures should be applied at multiple spatial scales to achieve the best spatially integrated and sustainable herbivore regulation impact because such a strategy would likely support the widest array of vertebrate and invertebrate herbivore natural enemies (Bommarco et al., 2012). Thirdly, the appropriate structural features and farming or cropping methods identified should be maintained across multiple cropping seasons rather than in the short term, so as to attract and retain sufficient populations of beneficial arthropods and birds.

6.5 General conclusions

The expected proliferation in population and variety of arthropod pests due to global warming presents a significant challenge to maize production worldwide but especially to those operating at small non-mechanized scale. Continuous and consistent application of pesticides is now known

to compound this problem because an increasing number of target herbivorous arthropod species are evolving resistance to various pesticides after prolonged exposure (Siegwart et al., 2015). At the same time, new technologies in seed improvement such as transgenic varieties remain beyond economic reach of most small-scale farmers, besides posing further risks of biological contamination to native biota (Castaldini et al., 2005; Andow, 2008; Tabashnik et al., 2013). This is however not to suggest that access to such biologically improved seeds necessarily promises total solutions to crop losses from arthropod herbivory; rather that farmers would be better off adopting locally available but effective measures in ameliorating the problem of crop damage. Therefore small scale farmers, already facing challenges of dis-economies of scale and low capacity to fight projected crop herbivory mediated by climate change, require simple and inexpensive yet effextive alternative solutions that help in minimizing crop damage while also conserving the integrity and health of the farming environment at affordable costs.

In this project, I have identified and highlighted a suite of key field management strategies that are suitable for small-scale maize farmers to foster natural regulation crop herbivory at the farm level, by attracting vertebrate and invertebrate natural enemies of pests. I show that when this range of farming systems, structural configuration and cover diversification methods are applied in synergistic concert, they constitute a form of conservation agriculture that can substantially improve overall habitat complexity to achieve a significantly integrated and sustainable strategy for pest biocontrol without compromising habitat and environmental health (Giacomo et al., 2012; Sain et al., 2017). Such farmer-based strategies are particularly crucial and relevant to subsistence maize farmers given the forecast of increased expenditure on pesticides to stave off impacts of pest proliferation due to climate change.

I emphasize however that sustainable gains in such natural herbivorous arthropod reduction strategies, just like in any integrated pest management system, would be best realized if local-level efforts are replicated and up-scaled at multiple spatial levels (Lichtenbert et al., 2017). This will enhance inter-farm spatial and functional connectivity for enhanced resilience against arthropod proliferations (Van den Berg and Ebenebe, 2001; Rusch et al., 2010; Inclan et al., 2015). Finally, as observed by Chaplin-Kramer et al. (2011), future studies on the ecosystem service function of herbivorous arthropod regulation by their natural enemies across farmlands should, in addition to predators-prey assemblage patterns at local or landscape scales, also delve deeper into comparative quantification of impacts of various predator functional groups on herbivory. This is significant because, while specialist and generalist predators respond differently to habitat variables at different spatial scales, herbivores mainly respond to local-scale effects of habitat management, structure and function. The use of stable isotope analysis, as demonstrated in chapter 3, would be a particularly instrumental and robust tool in elucidating such important interactions and would

reveal further details of predator-prey trophic associations crucial for informing efforts towards pest-resilient landscapes.

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Appendix 1. List of species and morpho species of arthropods collected from across the farms

Order	Family	*Scientific name*
Blattodea	Blattidae	*Blatella vaga*
Blattodea	Blattidae	*Blatella sp A*
Blattodea	Blattidae	*Blatella sp B*
Blattodea	Blattidae	*Blatella sp C*
Coleoptera	Acrididae	*Chorthippus brunneus*
Coleoptera	Cantharidae	*Rhangonycha spA*
Coleoptera	Carabidae	*Carabidae sp A*
Coleoptera	Carabidae	*Carabidae sp C*
Coleoptera	Carabidae	*Carabus sp A*
Coleoptera	Carabidae	*Carabus nemoralis*
Coleoptera	Carabidae	*Cychrus caraboides*
Coleoptera	Carabidae	*Gastrophysa viridula*
Coleoptera	Carabidae	*Laemostenus complanatus*
Coleoptera	Carabidae	*Laemostenus sp A*
Coleoptera	Carabidae	*Lebiinae sp A*
Coleoptera	Carabidae	*Strongylium purpuripenne*
Coleoptera	Carabidae	*Thermophilum sp A*
Coleoptera	Carnivorous	*Camponotus rufoglaucus*
Coleoptera	Chrysomelidae	*Chaetocnema purpurea*
Coleoptera	Chrysomelidae	*Chaetocnema sp A*
Coleoptera	Chrysomelidae	*Chaetocnema pulicaria*
Coleoptera	Chrysomelidae	*Chrysolina polita*
Coleoptera	Chrysomelidae	*Chrysolina sp A*
Coleoptera	Chrysomelidae	*Chrysolina sp B*
Coleoptera	Chrysomelidae	*Chrysomelidae sp C*
Coleoptera	Chrysomelidae	*Colasposoma cupricolle*
Coleoptera	Chrysomelidae	*Cryptocephalus coryli*
Coleoptera	Chrysomelidae	*Cryptocephalus spA*
Coleoptera	Chrysomelidae	*Deloyala sp A*
Coleoptera	Chrysomelidae	*Monolepta leuce*
Coleoptera	Chrysomelidae	*Monolepta qaudrizonata*
Coleoptera	Chrysomelidae	*Oulema melanopus*
Coleoptera	Chrysomelidae	*Sphaeroderma femoratum*
Coleoptera	Coccinellidae	*Cheilomenes lunata*
Coleoptera	Coccinellidae	*Cheilomenes sulphurea*
Coleoptera	Coccinellidae	*Cheilomes lunate*
Coleoptera	Coccinellidae	*Coccinella sp A*
Coleoptera	Coccinellidae	*Coccinellidae sp B*
Coleoptera	Coccinellidae	*Diomus sp A*
Coleoptera	Coccinellidae	*epilachna dregei*
Coleoptera	Coccinellidae	*epilachna multinota*
Coleoptera	Coccinellidae	*Henesepilachna reticulata*
Coleoptera	Coccinellidae	*Micraspis sp A*
Coleoptera	Coccinellidae	*Zicrona sp B*

Coleoptera	Curculionidae	*sitophilus zeamais*
Coleoptera	Formicidae	*camponotus sp D*
Coleoptera	Lagriidae	*Lagria villosa*
Coleoptera	Lycidae	*Lycus sp A*
Coleoptera	Meloidae	*Epicauta nyanssensis*
Coleoptera	Melyridae	*Malachius bipustulatus*
Coleoptera	Melyridae	*Malachius spA*
Coleoptera	Melyridae	*Melyriidae sp A*
Coleoptera	Melyridae	*Melyriidae sp B*
Coleoptera	Melyridae	*Mylabris bifasciata*
Orthopoptera	Formicidae	*Camponotus bayeri*
Coleoptera	Attelabidae	*Parapoderus nigripennis*
Coleoptera	Staphynilidae	*Scaphisoma sp A*
Coleoptera	Tenebrionidae	*Gonocephalum sp A*
Coleoptera	Tenebrionidae	*Gonocephalum sp B*
Coleoptera	Scolytidae	*Xylosandrus crassiusculus*
Dermaptera	Labiduridae	*Nala sp*
Dermaptera	Forficulidae	*Forficula auricularia*
Dermaptera	Spongiphoridae	*Labia sp*
Hemiptera	Aphididae	*Aphis sp*
Hemiptera	Aphididae	*Arbela carayoni*
Hemiptera	Aphididae	*Deraeocoris ostentans*
Hemiptera	Aphididae	*Rhopalosiphum maidis*
Hemiptera	Attelabidae	*Parapoderus nigripennis*
Hemiptera	Cercopidae	*Cercopidae sp C*
Hemiptera	Cicadidae	*Platypleura rutherfordi*
Hemiptera	Cicadidae	*Platypleura rutherfordi*
Hemiptera	Melyridae	*Anthocopus sp*
Hemiptera	Melyridae	*MelyriidaeA sp A*
Hemiptera	Miridae	*Proboscidocoris fulginoses*
Hemiptera	Pentatomidae	*Aurographa gamma*
Hemiptera	Pentatomidae	*Euschistus sp A*
Hemiptera	Pentatomidae	*Nezara viridua*
Hemiptera	Pentatomidae	*Zicrona sp A*
Hemiptera	Pentatomidae	*Zicrona caerulea*
Hemiptera	Pentatomidae	*Zicrona caerulea*
Hemiptera	Pentatomidae	*Zicrona caerulea*
Hemiptera	Pentatomidae	*Zicrona sp B*
Hemiptera	Pentatomidae	*Zicrona sp C*
Hemiptera	Tettigoniidae	*Microcentrum sp A*
Hemiptera	Tettigoniidae	*Microcentrum sp A*
Hemoptera	Aphididae	*Aphididae sp A*
Heteroptera	Nabidae	*Archibracon puchripinnis*
Homiptera	Flatidae	*Flatina rubrotincta*
Hymenoptera	Braconidae	*Apantales sesamiae*
Hymenoptera	Braconidae	*Apantales sp B*
Hymenoptera	Braconidae	*Archibracon dimaensis*
Hymenoptera	Braconidae	*Aspavia acuminata*

Hymenoptera	Braconidae	*Braconidae sp B*
Hymenoptera	Braconidae	*opydoaoma khoeleri*
Hymenoptera	Chalcididae	*Chalcis sp A*
Hymenoptera	Chalcididae	*Chalcis sp B*
Hymenoptera	Chalcididae	*Chalcis sp C*
Hymenoptera	Chalcididae	*Platytelenomus busseolae*
Hymenoptera	Eulophidae	*Pediobius furvus*
Hymenoptera	Eulophidae	*Goetheana sp*
Hymenoptera	Formicidae	*Anoplolepis steingroeveri*
Hymenoptera	Formicidae	*Camponotus bayeri*
Hymenoptera	Formicidae	*Camponotus chrysurus*
Hymenoptera	Formicidae	*Camponotus rufoglaucus*
Hymenoptera	Formicidae	*Camponotus sp A*
Hymenoptera	Formicidae	*Camponotus sp C*
Hymenoptera	Formicidae	*Camponotus sp D*
Hymenoptera	Formicidae	*Camponotus bayeri*
Hymenoptera	Formicidae	*Camponotus bimaculatus*
Hymenoptera	Formicidae	*Camponotus maculatus*
Hymenoptera	Formicidae	*Camponotus maculatus*
Hymenoptera	Formicidae	*Camponotus pompeus*
Hymenoptera	Formicidae	*Camponotus rofoclaucus*
Hymenoptera	Formicidae	*Camponotus sp A*
Hymenoptera	Formicidae	*Camponotus sp B*
Hymenoptera	Formicidae	*Camponotus sp C*
Hymenoptera	Formicidae	*Camponotus sp C*
Hymenoptera	Formicidae	*Camponotus sp D*
Hymenoptera	Formicidae	*Caponotus sp A*
Hymenoptera	Formicidae	*Carabera polita*
Hymenoptera	Formicidae	*Cataulacus pygmaeus*
Hymenoptera	Formicidae	*Cerebra polita*
Hymenoptera	Formicidae	*Crematogaster scutellaris*
Hymenoptera	Formicidae	*Crematogaster scutellaris*
Hymenoptera	Formicidae	*Crematogaster transiens*
Hymenoptera	Formicidae	*Decamorium decem*
Hymenoptera	Formicidae	*Dorylus spA*
Hymenoptera	Formicidae	*Lepisiota spA*
Hymenoptera	Formicidae	*Leptogenys spA*
Hymenoptera	Formicidae	*Meranoplus inermis*
Hymenoptera	Formicidae	*Monomorium spA*
Hymenoptera	Formicidae	*Myrmicaria opaciventris*
Hymenoptera	Formicidae	*Myrmicaria opaciventris*
Hymenoptera	Formicidae	*Odontomachus assiniensis*
Hymenoptera	Formicidae	*Odontomachus troglodytes*
Hymenoptera	Formicidae	*Pachycondyla ilgi*
Hymenoptera	Formicidae	*pachycondyla crassa*
Hymenoptera	Formicidae	*Pachycondyla ilgii*
Hymenoptera	Formicidae	*Pachycondyla subiridescens*
Hymenoptera	Formicidae	*Pachycondyla talpa*

Hymenoptera	Formicidae	*Pachycondyla tarsata*
Hymenoptera	Formicidae	*Paratrechina longicornis*
Hymenoptera	Formicidae	*Pheidole aurivillii*
Hymenoptera	Formicidae	*Pheidole megacephala*
Hymenoptera	Formicidae	*Pheidole pulchella*
Hymenoptera	Formicidae	*Polyrhachis militaris*
Hymenoptera	Formicidae	*Pristomyrmex africanus*
Hymenoptera	Formicidae	*Pyramica spA*
Hymenoptera	Formicidae	*Pyramica spA*
Hymenoptera	Formicidae	*Stigmatomma spA*
Hymenoptera	Formicidae	*Technomyrmex ilgii*
Hymenoptera	Formicidae	*Technomyrmex voeltzkowi*
Hymenoptera	Formicidae	*Tetramorium delagoense*
Hymenoptera	Formicidae	*Tetramorium edouardi*
Hymenoptera	Formicidae	*Tetramorium gazense*
Hymenoptera	Formicidae	*Tetramorium weitzeckeri*
Hymenoptera	Formicidae	*Tetramorium zonacaciae*
Hymenoptera	Ichneumonidae	*Ichneumolidae sp A*
Hymenoptera	Ichneumonidae	*Ichneumolidae sp A*
Hymenoptera	Ichneumonidae	*Iphiaulax sp A*
Hymenoptera	Ichneumonidae	*Iphiaulax sp C*
Hymenoptera	Mymaridae	*Alaptus sp*
Hymenoptera	Sapygidae	*Sapygina sp A*
Hymenoptera	Scelionidae	*Pediobius sp A*
Hymenoptera	Scelionidae	*Platytelenomus brunneus*
Hymenoptera	Scelionidae	*Scelionidae sp A*
Hymenoptera	Scoliidae	*ScoliidaeA sp A*
Hymenoptera	Proctotrupoidea	*Platytelenomus sp B*
Isoptera	Termitidae	*Macrotermes sp A*
Lepidoptera	Arctiitae	*ArctiitaeA sp A*
Lepidoptera	Geometridae	*GeometridaeB sp C*
Lepidoptera	Hepiadidae	*Hepiadidae sp C*
Lepidoptera	Lasiocampidae	*Lasiocampidae sp C*
Lepidoptera	Noctuidae	*Bembidion sp*
Lepidoptera	Noctuidae	*Busseola fusca*
Lepidoptera	Noctuidae	*Callosobruchus maculatus*
Lepidoptera	Noctuidae	*Chilo partellus*
Lepidoptera	Noctuidae	*Chilo s pA*
Lepidoptera	Noctuidae	*Noctiodae sp A*
Lepidoptera	Noctuidae	*Noctiodae sp B*
Lepidoptera	Noctuidae	*Noctuidae sp C*
Lepidoptera	Noctuidae	*Noctuidal sp C*
Lepidoptera	Noctuidae	*Phodia interpunctella*
Lepidoptera	Noctuidae	*Plusinae sp A*
Lepidoptera	Nymphalidae	*Nymphalidae sp A*
Lepidoptera	Nymphalidae	*Nymphalidae sp B*
Lepidoptera	Papilionidae	*Charaxes tiridates*
Mantodae	Mantidae	*Mantis sp*

Neuroptera	Chrysopidae	*Chrysopa spA*
Neuroptera	Chrysopidae	*Italochrysa variegata*
Neuroptera	Hemerobiidae	*Micromus sp A*
Neuroptera	Hemerobiidae	*Micromus sp B*
Orthoptera	Acrididae	*Abisares viridipennis*
Orthoptera	Acrididae	*Acanthacris ruficornis*
Orthoptera	Acrididae	*Acridicae sp C*
Orthoptera	Acrididae	*Acrididae sp A*
Orthoptera	Acrididae	*Acrididae sp B*
Orthoptera	Acrididae	*Chirthoppus brunneus*
Orthoptera	Acrididae	*Eyeprepocnemis plorans*
Orthoptera	Acrididae	*Heteractis vinacea*
Orthoptera	Acrididae	*Paracoptacra cauta*
Orthoptera	Acrididae	*Parasphena mauensis*
Orthoptera	Acrididae	*Schistocerca sp A*
Orthoptera	Acrididae	*Serpusia lamerineli*
Orthoptera	Attelabidae	*Parapoderus spA*
Orthoptera	Cicadellidae	*tettigoniella blandula*
Orthoptera	Grylloidae	*Gryllus auricularia*
Orthoptera	Grylloidae	*Gryllus bimaculatus*
Orthoptera	Grylloidae	*Gryllus sp A*
Phasmadodea	Timematidae	*Timema sp*
Thysanoptera	Thripidae	*Frankiniella williamsii*
Thysanoptera	Thripidae	*Thrips angusticeps*

Appendix 2: Checklist of birds encountered during the surveys across the farms. The list follows the nomenclature in Zimmerman et al. (1996).

Family	Common name	Scientific name	Guild
Apodidae	African black Swift	*Apus barbatus*	Insectivore
	Little Swift	*Apus affinis*	Insectivore
Columbidae	Blue-spotted Wood Dove	*Turtur afer*	Herbivorous
	Mourning Dove	*Zenaida macroura*	Herbivorous
	Red-eyed Dove	*Streptopelia semitorquata*	Herbivorous
	Ring-necked Dove	*Streptopelia capicola*	Herbivorous
	Speckled Pigeon	*Columba guinea*	Herbivorous
	Tambourine Dove	*Turtur tympanistria*	Herbivorous
Cuculidae	African common Cuckoo	*Cuculus canorus*	Insectivore
	African Cuckoo	*Cuculus gularis*	Insectivore
	Diedrick Cuckoo	*Chrysococcyx caprius*	Insectivore
	Klaas Cuckoo	*Chrysococcyx klaas*	Insectivore
	Red-chested Cuckoo	*Cuculus solitarius*	Insectivore
	White-browed Coucal	Centropus superciliosus	Insectivore
Musophagidae	Eastern Plantain-eater	*Crinifer zonurus*	Herbivorous
Coliidae	Speckled Mousebird	*Colius striatus*	Generaliste
Meropidae	Cnnamon-chested Beeeater	*Merops oreobates*	Insectivore
	Eurasian Beeeater	*Merops apiaster*	Insectivore
	Little Beeeater	*Merops pusillus*	Insectivore
	White-fronted Beeeater	*Merops bullockoides*	Insectivore
	White-throated Beeeater	*Merops albicollis*	Insectivore
Bucerotidae	Black-and-white casqued Hornbill	*Bycanistes subcylindricus*	Herbivorous
Lybiidae	Double-toothed Barbet	*Lybius bidentatus*	Herbivorous
	Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	Insectivore
Dendropicos	Cardinal Woodpecker	*Dendropicos fuscescens*	Insectivore
Indicatoridae	Lesser Honeyguide	*Indicator minor*	Insectivore
Hirundinidae	Barn Swallow	*Hirundo rustica*	Insectivore
	Black Saw-wing	*Psalidoprocne pristoptera*	Insectivore
	Red-rumped Swallow	*Cecropis daurica*	Insectivore
	White-headed Saw-wing	*Psalidoprocne albiceps*	Insectivore
	Wire-tailed Swallow	*Hirundo smithii*	Insectivore
Motacillidae	Cape Wagtail	*Motacilla capensis*	Insectivore
	Pied Wagtail	*Motacilla aguimp*	Insectivore
	Yellow Wagtail	(Motacilla flava	Insectivore
Pycnonotidae	Common Bulbul	*Pycnonotus barbatus*	Generalist
	Bristlebill	*Bleda sp.*	Insectivore
	Honey-guide Greenbul	*Baeopogon indicator*	Generalist
	Yellow-throated Leaflove	*Atimastillas flavicollis*	Insectivore
	Honey-guide Greenbul	*(Baeopogon indicator*	Generalist

Turdidae	African Thrush	*Turdus pelios*	Insectivore
	Grey-capped Warbler	*Eminia lepida*	Insectivore
	Grey-backed Camaroptera	*Camaroptera brevicandata*	Insectivore
	Rattling Cisticola	*Cisticola chiniana*	Insectivore
	Red-faced Cisticooa	*Cisticola erythrops*	Insectivore
	Shifling Cisticola	*Cisticola brachypterus*	Insectivore
Cisticolodae	Singing Cisticola	*Cisticola cantans*	Insectivore
	Stout Cisticola	*Cisticola robustus*	Insectivore
	Tawny-flanked Prinia	*Prinia subflava*	Insectivore
	Trilling Cisticola	*Cisticola woosnami*	Insectivore
	WindingCisticola	*Cisticola galactotes*	Insectivore
	Yellow-breasted Apalis	*Apalis flavida*	Insectivore
	Zitting Cisticola	*Cisticola juncidis*	Insectivore
Phylloscopidae	Willow Warbler	*Phylloscopus trochilus*	Insectivore
Sylviidae	Garden Warbler	*Sylvia borin*	Insectivore
	African dusky Frycatcher	*Muscicapa adusta*	Insectivore
	Common Stonechat	*Saxicola rubicola)*	Insectivore
	Little grey Flycatcher	*Muscicapa epulata*	Insectivore
Muscicapidae	Northern black Flycatcher	*Melaenornis edolioides*	Insectivore
	Pale Flycatcher	*Melaenornis pammelaina*	Insectivore
	White-browed Robin Chat	*Cossypha heuglini*	Insectivore
	White-eyed slaty Flycathcer	*Melaenornis fischeri*	Insectivore
Dicruridae	Common Dongo	*Cuculus canorus*	Insectivore
Pellorneidae	Brown Illadopsis	*Illadopsis fulvescens*	Insectivore
Platysteridae	Brown-throated Wattle-eye	*Platysteira cyanea*	Insectivore
	Chin-spot Batis	*Batis molitor*	Insectivore
Leiothrichidae	Arrow-marked Babbler	*Turdoides jardineii*	Insectivore
	Golden-winged Sunbied	*Drepanorhynchus reichenowi*	Herbivorous
	Beautiful Sunbird	*Cinnyris pulchellus*	Herbivorous
Nectariniidae	Northern double-collared Sunbird	*Cinnyris reichnowi*	Herbivorous
	Bronze Sunbird	*Nectarinia kilimensis*	Herbivorous
	Ggreen-headed Sunbird	*Cyanomitra verticalis*	Herbivorous
	Variable Sunbird	*Nectarinia venusta*	Herbivorous
	African yellow White-eye	*Zosterops senegalensis*	Insectivore
Zosteropidae	Common White-eye	*Zosterops palpebrosus*	Insectivore
	Montane White-eye	*Zosterops poliogaster*	Insectivore
	Baglafecht Weaver	*Ploceus baglafecht*	Generalist
	Grosbeak Weaver	*Amblyospiza albifrons*	Generalist
Ploceidae	Holub's golden Weaver	*Ploceus xanthops*	Generalist
	Spectacled Weaver	*Ploceus ocularis*	Generalist
	Village Weaver	*Ploceus cucullatus*	Generalist
Monarchidae	African grey Flycatcher	*Terpsiphone viridis*	Insectivore

	African grey Flycatcher	*Empidonax wrightii*	Insectivore
Stenostiridae	African blue Flycatcher	*Elminia longicauda*	Insectivore
	White-tailed crested Flycatcher	*Elminia albonotata*	Insectivore
Sturnidae	Black-headed Apalis	*Apalis melanocephala*	Insectivore
	Greater blue-eared Starling	*Lamprotornis chalybaeus*	Insectivore
Laniidae	Common Fiscal	*Lanius collaris*	Insectivore
	Long-tailed Fiscal	*Lanius cabanisi*	Insectivore
Malaconotidae	Sulphu-breasted Bush-shrike		Insectivore
Lybiidae	Tropical Boubou	*Laniarius aethiopicus*	Insectivore
Tinaliidae	White-browed Coucal	*Centropus superciliosus*	Insectivore
Paridae	White-bellied Tit	*Parus albiventris*	Insectivore
Passeridae	Grey-headed Tparrow	*Passer griseus*	Generalist
	House Sparrow	*Passer domesticus*	Generalist
Estrildidae	African Firefinch	*Lagonosticta rubricata*	Herbivorous
	Black-and-white Mannikin	*Lonchura bicolor*	Herbivorous
	Bronze Mannikin	*Lonchura cucullata*	Herbivorous
	Red-cheeked Cordonbleau	*Uraeginthus bengalus*	Herbivorous
	Village Indigobird	*Vidua chalybeata*	Herbivorous
Viduidae	Pin-tailed Whydah	*Vidua macroura*	Insectivore
	Village Indigobird	*Vidua chalybeata*	Insectivore
Carduelinae	Streaky Seedeater	*Crithagra striolatus*	Herbivorous
Fringillidae	African Citril	*Crithagra citrinelloides*	Herbivorous